DETERMINANTS OF THE DIFFERENCE IN FORAGE QUALITY BETWEEN
PENSACOLA BAHIAGRASS (*Paspalum notatum* Flugge) AND MOTT
DWARF ELEPHANTGRASS (*Pennisetum purpureum* Schum.)

BY

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To my family
Gladys, Fabricio and Valeria

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Under grazing, Mott dwarf elephantgrass (MDE) supports higher
average daily gains than does Pensacola bahiagrass (PB). The objective
was to compare MDE with PB in terms of chemical composition, leaf
anatomy, intake, digestibility, mastication patterns and rumen kinetics,
when both were harvested after equal regrowth intervals in June (J) and
September (S), in order to find explanations for the superiority of MDE
in forage quality.

Plots of PB and MDE were sampled at 3, 5 and 7 wk of regrowth in J
and S. Nitrogen concentration and in vitro organic matter digestion
(IVOMD) were higher, and neutral-detergent fiber (NDF) and lignin
concentrations were lower for MDE than for PB. There was no season
effect except that IVOMD of PB was higher during S.

Five-wk regrowths of PB and MDE harvested in J and S were fed for
4 h daily (0800-1200) at the same level of NDF intake (g/kg $BW^{.75}$) to
four ruminally-fistulated sheep. During eating, frequency of chewing

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and rate of intake were higher for MDE. During rumination, jaw movement counts, time spent per bolus and per kg of organic matter (OM) and NDF consumed, and rumination index (jaw movements/100 g OM on a BW basis) were lower for MDE. Pre-feeding large-particle (>1.18 mm, LP) and pre- and post-feeding small-particle pools were smaller for MDE. Particle size reduction during eating was similar for both grasses, but tended to be lower (P=.14) for PB during rumination. Disappearance of ruminal OM, NDF and indigestible NDF during eating was the same for both grasses, but larger proportions of the existing pools of OM and NDF disappeared between meals for MDE.

Twenty-four sheep were fed the four hays ad libitum and dosed orally with Cr-mordanted small particles (Cr-SP) collected from the rumen (pre-feeding). Digestibilities of OM and NDF were higher for MDE. Total OM and digestible OM and NDF intakes were higher for MDE, and for both grasses, were higher for J harvests. For PB, digestible OM intake was below maintenance for S. Mean retention time (MRT) of Cr-SP tended to be shorter (P=.12) for MDE, and was longer for S harvests. Negative relationship was found between Cr-SP MRT and OM intake (-.57, P=.004, n=24). Undigestible linkages between the epidermis and vascular bundles by means of highly lignified sclerenchyma fibers were observed in PB but not in MDE.

Mott may have had higher digestibility and intake relative to Pensacola because its anatomical structure was more accessible to microorganisms during digestion, its undigested residues were less resistant to particle comminution during rumination, and its small particles tended to have lower MRT.

Increasing demands for milk and meat have required progressive advancement in animal and forage production systems. Improving the efficiency of use of land and forage resources can result in higher levels of animal production per unit of area. Environmental conditions existing in tropical and subtropical areas of the world, however, make such improvements difficult to attain. Introduction of high-quality adapted species of grasses in tropical areas is one approach to minimizing the negative impact of environment on productivity of forage-livestock systems.

'Mott' dwarf elephantgrass (*Pennisetum purpureum* Schum.) has significant potential to support high levels of animal performance throughout the grazing season, even under environmental conditions which affect other tropical grasses to the extent that they are unable to meet the maintenance requirement of grazing livestock. High forage quality of Mott can be the result of high nutritive value and (or) high levels of voluntary intake by grazing animals. Chemical analyses and in vitro determinations of potential digestibility have revealed the superiority in nutritive value of Mott over other tropical grasses. Knowledge about voluntary intake when Mott is grazed or fed to individual animals is, however, limited.

Evidence exists in the literature that most of the difference in forage quality among grasses can be explained at the micro-anatomical level of plant composition. Proportions of highly fermentable tissues like mesophyll and phloem can be related to potential digestibility, and the proportions of rigid tissues like epidermis and sclerenchyma fibers can determine resistance characteristics of grasses to particle comminution by mastication. Differences in dynamics of microbial fermentation and its contribution to digesta particle fragility, specific gravity and retention time may explain differences in intake among grasses.

The present work was designed to elucidate some of the reasons for the high level of forage quality observed in Mott. Chemical composition, plant anatomy, nutritive value, intake, and nutritional physiology were studied in sheep fed Mott and Pensacola bahiagrass, the latter being a common improved forage grass species used in the southeastern USA.

CHAPTER II
LITERATURE REVIEW

Pensacola Bahiagrass

General

'Pensacola' bahiagrass (*Paspalum notatum* Flugge) is an important
source of forage in tropical and subtropical areas of the world (Sampaio
and Beaty, 1976) and represents the predominant warm-season perennial
grass grown in the southeastern USA (Evers, 1985). Pensacola is a tough
competitor which forms an extremely dense sod, crowded with stubby
stolons (Kalmbacher et al., 1980). In Florida it produces about 75% of
its annual dry matter (DM) yield from May to October, but growth ceases
when soil temperature falls below 15°C (Kalmbacher et al., 1980; Sampaio
and Beaty, 1976). It is tolerant of heavy continuous grazing, a
management that will result in loss of stands of many other warm-season
perennials (Sollenberger et al., 1988b).

Effect of Environmental Conditions

Light and temperature seem to have a more pronounced effect on
seasonal patterns of DM accumulation than do N source or application
procedure (Santana et al., 1982). Stage of physiological maturity is
known to be influenced by environmental conditions that result in
differences in growth and chemical composition of warm-season grasses
(Henderson and Robinson, 1982a; Ferraris et al., 1986).

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Even though increases in neutral-detergent fiber (NDF) and decreases in NDF digestibility have resulted from increases in temperature (Wilson and Minson, 1980), Henderson and Robinson (1982a) found that high temperature produces lower concentrations of NDF in Pensacola, and that the effect of temperature on lignin depends on incidental light. Temperature and light affect fiber components differently, and the intensity of their effect depends upon the fiber fraction, the grass species, and soil moisture (Henderson and Robinson, 1982a). Drought reduces in vitro organic matter digestibility (IVOMD) and N availability, thus reducing intake (McMeniman et al., 1986).

In north Florida, like in most of the southeastern USA, the climate during the growing season is characterized by considerable fluctuations in temperature, solar radiation, and rainfall (McCloud and Hill, 1987). Growth rate of most tropical grasses increases with temperature and intensity of light (Wilson and Minson, 1980), but conditions favoring maximum growth have frequently resulted in reduced forage quality (Minson, 1980; Henderson and Robinson, 1982b; Akin et al., 1987). These reports support the need to consider environmental factors related to seasons of growth when evaluating differences in quality of warm-season perennial grasses.

Nutritive Value and Animal Performance

Under continuous grazing and variable stocking rate Pensacola showed high average daily gain (ADG; 1.0 kg) at the beginning of the grazing season (May), but it decreased to -.52 during September (Prates et al., 1974). The decline in animal performance ("summer slump") reduced also animal production per hectare (Prates et al., 1974). A

slump in animal performance by the end of the summer has been observed frequently with Pensacola (Sollenberger et al., 1988a; Pitman et al., 1984) and also with other tropical grasses (Rusland et al., 1988; Sollenberger et al., 1988a).

Under rotational grazing and N fertilization, ADG of steers grazing Pensacola was .38 kg, average stocking rate was approximately four animals per hectare, and production per year was 318 kg/ha. Under this more intensive management, steers grazing Pensacola also exhibited the summer slump, which was related to lower herbage IVOMD and N concentration (Sollenberger and Jones, 1989). In this experiment ADG was equal or superior to most of the values reported in the literature for Pensacola.

Explanations for the summer slump have included lower nutritive value of the grass due to increased lignification, environmental stress, high stocking rates, and underutilization of forage. Under continuous stocking, Pensacola did not differ in animal performance from 'Floralta' limpograss [*Hemarthria altissima* (Poir.) Stapf et C.E. Hubb.], although, extrusa samples had lower IVOMD and higher N concentrations than did Floralta (Sollenberger et al., 1988a). Indirect estimations of voluntary intake have indicated a reduction in intake from May to September (Prates et al., 1974). Because ADG started to decrease in June, it is possible that high temperature during the summer months had a negative effect upon animal response, and that the high precipitation during July contributed to the decreased gain during the following periods (Prates et al., 1974). Prates et al. (1974) considered that the decreased gain during summer was not due to a lack of available forage.

Mott Dwarf Elephantgrass

General

'Mott' dwarf elephantgrass (*Pennisetum purpureum* Schum.) was introduced into Florida from Tifton, Georgia, in 1977. Mott is a perennial grass that persists for many years if managed properly. Mott was selected from among a selfed progeny of 'Merkeron' elephantgrass and released as Tift N75 dwarf napiergrass germplasm by the USDA Coastal Plain Experiment Station in 1986 (Sollenberger et al., 1988c).

In a recent publication, Sollenberger et al. (1988c) have reviewed all aspects related to establishment, yield, forage quality, fertilization and pests. They pointed out that Mott has to be propagated vegetatively using stem cuttings and requires some basic fertilization consisting of N, phosphorus, potassium and micronutrients. Mott is better established in moderately well-drained to well-drained soils, and elimination of weeds is important. Mott DM yields compared well with those obtained for other tropical forages commonly found in Florida, and at a very advanced maturity (10 wk of regrowth) leaf percentage was 65% of DM (Boddorff and Ocumpaugh, 1985).

Nutritive Value and Animal Performance

Crude protein concentration was superior in Mott compared to that of limpograss, bermudagrass [*Cynodon dactylon* (L.) Pers.], stargrass (*Cynodon nlemfuensis* Vanderyst) and digitgrass (*Digitaria* X *umfolozi* Hall) either during the summer or fall (Kalmbacher et al., 1987). Organic matter digestibility was similar during the summer for all grasses, but higher in the fall for Mott compared to others. This

superiority in nutritive value during the fall may explain partially the higher levels of animal performance on Mott throughout the grazing season and why the other grasses exhibit the summer slump.

Sollenberger et al. (1988b; 1989) and Sollenberger and Jones (1989) demonstrated the high forage quality of Mott compared to Pensacola. Daily gains in animals grazing Mott averaged .97 kg over 3 grazing seasons. This level of animal performance has not been achieved by any of the common tropical grasses used in the southeast USA. Gain per ha averaged 483 kg/yr, although Mott stocking rate tended to be lower than that of Pensacola. Over 3 years mean DM accumulated was 8.2 MT/(ha·yr) (Sollenberger and Jones, 1989). Hand-plucked samples confirmed that IVOMD and CP concentrations were consistently higher for Mott than for Pensacola, and IVOMD was similar to that of rhizoma peanut (Sollenberger et al., 1989). The striking aspect was that Mott maintained IVOMD of nearly 70% throughout the grazing season (Sollenberger and Jones, 1989).

Desirable attributes of Mott include high leaf:stem ratio even at very advanced ages of regrowth (Boddorff and Ocumpaugh, 1985), high DM production (Kalmbacher et al., 1987), high leaf IVOMD and CP at 35 d regrowth (Boddorff and Ocumpaugh, 1985) and persistence under grazing when well managed (Sollenberger et al., 1988c). Lower susceptibility of Mott to environmental changes may be related to its anatomical structure and rate of metabolism.

A tropical grass with exceptional characteristics of forage quality, like those shown by Mott, gives researchers an opportunity to analyze and understand the reasons or causes of low forage quality of

other tropical grasses. This research should be based in simultaneous
comparative studies of the chemical and physical differences between
grasses, and be projected to develop methods to improve the quality of
other tropical grasses.

Forage Quality

According to Moore and Mott (1973) forage quality is best defined
as the level of animal performance when forage availability is not
limiting, animal potential for gain exists and does not vary between
treatments, and no supplement is offered. Under the described
condition, differences in forage quality will result from differences in
voluntary intake and (or) nutritive value (Mott, 1959).

Forages are used by ruminants as a source of energy, and for that
reason the nutritive value of a forage is better expressed in terms of
its digestible energy concentration (Moore and Mott, 1973). Close
relationships exist between digestible energy and digestible organic
matter (OM) or total digestible nutrients, the last two being more
practically determined in digestion trials. As forage quality results
from the product of nutritive value and intake, its best expression is
in terms of digestible OM intake.

Voluntary intake, digestibility, and efficiency of nutrient
utilization determine forage quality (Moore and Mott, 1973; Minson,
1980). For many forages, more of the variability in forage quality can
be explained by changes in voluntary intake than by changes in
digestibility (Moore and Mott, 1973; Wilson and Minson, 1980). Thus,

intake is a critical response to be measured when evaluating forage quality.

Voluntary Intake

Voluntary intake is defined as the quantity of feed an animal will consume when availability of that feed is not limiting. Difficulties exist when determining voluntary intake with grazing animals. Some indirect methods have been used, but they render only close estimates rather than accurate measurements. Therefore, pen-fed animals are more frequently used to determine voluntary intake and digestibility. When measured with pen-fed animals, voluntary intake has been defined as the amount of feed eaten when a 15% excess is offered (Blaxter et al., 1961).

Control Mechanisms

The central nervous system controls feed intake in animals (Baile and Forbes, 1974; NRC, 1985). In ruminants, intake is controlled by hunger-satiety systems (Campling, 1970) that involve hormones and other metabolites to set the initiation and termination of a meal (Forbes, 1980; Baile et al., 1983). In the long term, feed intake in ruminants is controlled by two basic mechanisms: metabolic or physical (Conrad, 1966; Forbes, 1980). Based on relationships observed between intake and digestibility, Blaxter et al. (1961) proposed that a change in the type of control mechanism occurred when energy digestibility exceeded 70%, but it may not be such a precise point. It has been suggested that both mechanisms are involved in regulating intake throughout the whole range

of diets utilized by ruminants with gradual predominance of one over the other (Egan, 1970).

With tropical forages the physical or distention control mechanism is mainly regulating intake. Under physical control, intake will terminate when the volume of rumen content reaches a certain critical level recognized as the filling effect (Crampton et al., 1960; Blaxter et al., 1961; Montgomery and Baumgardt, 1965; Grovum and Phillips, 1978).

Rumen Fill

Blaxter et al. (1961) proposed that sheep consume roughage diets to a constant level of fill in the rumen, irrespective of the type of forage. The concept of rumen fill has been consistently supported in the literature by the work of Freer and Campling (1963), Minson (1966), Laredo and Minson (1973) and Poppi et al. (1981).

Due to the fact that changes in weight rather than changes in volume of rumen fill explained most of the variation in voluntary intake, intake has been related more to the quantity of DM in the rumen (McClung, 1983) and the time it is retained (Van der Aar et al., 1983). Some physiological conditions like pregnancy, lactation, and cold exposure can temporarily affect rumen fill, but animals will tend to compensate for the new physiological status by changes in the rate of rumen content removal or intake (Thornton and Minson, 1973).

Mechanisms of Rumen Fill Release

Rumen fill can be released by digestion and absorption of fermentable OM in the rumen or by passage out of the rumen of undigested material. The rate and extent of digestion will depend on the chemical composition and spatial distribution of nutrients within the plant anatomical structure, and accessibility of structures to microorganisms (Akin, 1986; Grenet, 1989). On the other hand, the rate of disappearance of undigested material is a function of the rate of breakdown of digesta to a form suitable for escape from the reticulo-rumen (Ulyatt et al., 1986).

Microbial digestion in the rumen

Rumen digesta contain large numbers of bacteria and protozoa. Their population size and species groups depend on the diet. After deglutition of masticated feed particles, colonization takes place almost immediately within a range of 5 min to 2 h (Akin, 1986; Bauchop, 1979). Large numbers of bacteria adhere strongly to feed particles (Akin, 1979). Attachment to forage cell walls varies depending on the bacterial species (Akin, 1976). However, it seems that bacteria are able to digest mesophyll and phloem tissues without attachment. Attachment seems to be more important for the degradation of other less-degradable tissues (Akin et al., 1974a; Akin and Amos, 1976).

In addition to bacteria, protozoa and fungi have important actions, in spite of their relatively small number. Fungi rapidly colonize the plant vascular tissue, and because of that a high relationship has been found between fibrousness of diet and fungi population (Bauchop, 1979). The main effect of anaerobic fungi is the

disruption of plant tissues, which aids the rumen bacteria to colonize the particles, thus speeding up fiber digestion (Orpin, 1984).

Size of fungal populations depends markedly on the sulfur content in the feed (Akin and Hogan, 1982). Akin and Hogan (1982) proposed that weakening of lignified tissue by fungal attack may explain the increase in intake of sulfur-fertilized Digitaria [*Digitaria pentzii* (Stent)]. Sulfur does not alter plant anatomy (Akin and Hogan, 1982), but fungal attack softens lignified tissues reducing resistance to fracture and increasing intake (Akin et al., 1983). Rumen microorganisms colonize plant material primarily through the broken or cut surface of leaves (Monson et al., 1972). Fungi, on the other hand, can also penetrate through the stomata by their rhizoids (Akin et al., 1983).

Cell-wall composition and structure have been recognized as factors influencing cell-wall digestion (Baile and Jones, 1971). Differences in microanatomy could be factors responsible for variation in the digestibility of grasses (Akin and Burdick, 1973). Cutinized epidermis and lignified tissues (vascular bundles and sclerenchyma) resist microbial digestion and are excreted undigested. Mesophyll and phloem are digested more rapidly than other digestible cell walls (Akin et al., 1973) and more rapidly digested in temperate than in tropical grasses (Akin et al., 1973). Lignified tissues like sclerenchyma had a low propensity for bacterial attachment (Akin et al., 1974b) and are usually not digested (Akin et al., 1973).

Histochemical studies (Vance et al., 1980) demonstrated that there are different types of lignified tissue which possess different abilities to resist microbial digestion. Acid Phloro-glucinol-positive

tissues totally resist attack and are normally present in the inner bundle sheath and xylem cell walls. On the other hand, Chlorine-sulfite-positive tissues, which are present in the sclerenchyma (Akin and Burdick, 1975; Akin et al., 1977) are less resistant to microbial digestion than are lignified tissues (Akin, 1980, 1982a, 1982b). Akin and Burdick (1975) classified plant tissue into three categories: a) rapidly digested (mesophyll and phloem), b) slowly digested (epidermis and parenchyma bundle sheath) and c) indigestible (sclerenchyma and vascular tissue).

Digesta turnover

Digesta escapes through the reticulo-omasal orifice and is expelled out of the rumen by coordinated movements of the reticulo-rumen (Reid, 1963) and omasum (Stevens et al., 1960). In order to pass, digesta particles must be reduced in size by chewing during eating and rumination, microbial digestion and detrition (Reid et al., 1977; McLeod, 1986). Reduction in size is mainly achieved by mastication during eating and rumination (Balch and Campling, 1962) with the main role played by rumination (Gordon, 1965).

Swallowed ingesta entering the reticulo-rumen follows one of two paths depending on size and specific gravity. Dense material sinks in the fluid digesta in the reticulum. More light material floats in the liquid phase until the next reticular contraction propels them into the dorsal sac of the rumen (Reid, 1963). Thus, boli of feed become mixed with digesta mass a few minutes after swallowing (Magee, 1932).

From both processes of mastication, rumination plays a more important role in influencing the rate of removal of DM from the rumen.

Rumination is an important process in reducing particle size in the rumen, and at the same time it influences water flow through the rumen by means of its effect on salivary secretion (Ulyatt, 1983; Ulyatt et al., 1986). Passage of digesta out of the rumen will depend on the flow per contraction (Ulyatt et al., 1984) and amplitude of reticular contraction (Okine et al., 1989), rather than on changes in the contraction rate (Ulyatt, 1983).

Passage of digesta through the reticulo-omasal orifice depends on the closeness of particles to the orifice. Therefore, the transfer of particles from the solid mass of digesta to the fluid close to the reticulo-omasal orifice seems to be one of the most important steps governing passage (Balch, 1960). It is possible that specific gravity can be a critical determinant for this transfer. The importance of specific gravity in determining mean retention time has been demonstrated (Campling and Freer, 1962; Murphy et al., 1989). Differences in flow of particles in the rumen are inversely related to specific gravity in a range of 1.02 to 1.40. However, in any analysis of the effect of specific gravity of particles on rumen kinetics, the specific gravity of rumen digesta has to be considered also. Large particles tend to have lower specific gravity than do small particles, and a relationship between particle size and specific gravity has been detected independent of forage source (Evans et al., 1973; Murphy et al., 1989). Water saturation and microbial digestion increase specific gravity and consequently increase the tendency of particles to sink into the ventral sac. During fermentation gas is produced, however, and it may be entrapped in the particles, reducing their specific gravity.

In order to leave the rumen and maintain intake, digesta particles must be reduced in size. Cattle possess a slightly larger reticulo-omasal orifice than do sheep, but both appear sufficiently large to allow the passage of most feed particles from the rumen. There is a discrimination process against large particles, however, with only particles less than a certain critical size being able to readily leave the rumen (Evans et al., 1973; Reid et al., 1977; Poppi et al., 1980, 1985). The resistance to escape of the smaller particles also varies with particle size (Poppi et al., 1980).

The omasum appears to play a role in retaining large particles in the rumen. Large particles have been found in the omasum of cattle but not in the abomasum (Poppi et al., 1980). No significant reduction in particle size appears to occur between the abomasum and the feces (Poppi et al., 1980, 1985; Uden and Van Soest, 1982). Because particles larger than 10 mm appear in the omasum, and back flow of digesta to reticulum is smaller compared to the flow from the reticulum, McBride et al. (1984) proposed that the control of the digesta transit may originate from the sorting and physical stratification of digesta particles in the rumen with the omasum returning large particles to the rumen.

Sieving mechanisms based on the entrapment of particles in the fibrous mat of digesta have been reported by Faichney (1986). Faichney (1986) showed that more than 50% of small particles which would be expected to leave the rumen were entrapped in the rumen filter bed.

Digesta particles in the rumen are at different stages of breakdown in a continuum of particle size (Faichney, 1986). From many methods used to analyze particle size, the most appropriate appears to

be that which divides the particulate phase into two pools of large and small particles (Mertens and Ely, 1979; Poppi et al., 1980). Large particles are important because they influence rumination behavior, and small particles represent the part of the rumen solids capable of easily escaping from the rumen (Mertens et al., 1984). Through wet sieving Poppi et al. (1980) defined an aperture size of 1.18 mm as that which can be used to separate the two particle pools.

Evidence suggests that breakdown of large particles during rumination is a rate-limiting step in the removal of undigested DM from the rumen (Reid et al., 1979; Ulyatt, 1983; Ulyatt et al., 1986), although Poppi et al. (1981) proposed that the factor limiting the rate of DM passage from the rumen was the rate of small particle removal and not the rate of breakdown of large particles during rumination. Faichney (1986) and Waghorn et al. (1986) found that a large proportion of the small particles in the rumen are retained in the digesta mass of large particles through the filter bed effect. Ulyatt et al. (1986) suggested that rumination in addition to reducing particle size also has an important role in conjunction with rumen movements in the process of streaming and sorting out digesta and contributes to the removal of digesta from the reticulum.

Mastication Patterns

Eating

The extent of large particle breakdown by primary mastication during eating depends on the chemical composition (Nelson, 1988), type of forage and level of intake (Waghorn et al., 1986), and on individual characteristics of the experimental animals (Lee and Pearce, 1984).

Extensive breakdown occurs with high-quality temperate forages (Reid et al., 1979; Ulyatt, 1983), while less breakdown occurs with mature temperate grasses (Lee and Pearce, 1984) or tropical forages (Poppi et al., 1981).

Fatigue is unlikely to influence the voluntary intake of pen-fed animals (Campling and Balch, 1961), although it limits the time spent eating by grazing animals to about 720 min/d (Stobbs, 1974). Eating time decreases with advancing plant maturity resulting in decreased voluntary intake and digestibility (Dulphy and Demarquilly, 1974).

Time spent eating fresh grass is longer than for the corresponding hay (Fujihara, 1980), perhaps because fresh grass is more difficult to make into a bolus for swallowing than is hay (Fujihara, 1980). The same reasons are used to explain differences in levels of intake between hays and silage prepared from the same species (Fujihara, 1982).

Eating rate (g DM/min) has been shown to be a highly repeatable measurement of ingestive characteristics of a given source of forage (Ulyatt et al., 1986) and is highly correlated with voluntary intake (Balch and Campling, 1962; Forbes et al., 1972). Eating rate may be affected, however, by processing (grinding and pelleting) (Forbes et al., 1972), or by environmental conditions like cold stress (Kennedy, 1983). Kennedy (1983) reported a faster rate of intake under cold conditions.

Rumination

During rumination, regurgitated material arrives in the mouth, and liquids and a large proportion of small particles are immediately reswallowed (Deswysen and Ehrlein, 1981), enhancing the proportion of

large particles in the material retained in the mouth (Chai et al., 1984; Kennedy, 1985). The retained bolus is remasticated, reinsalivated and then reswallowed.

Ruminants spend an average of 6-7 h/d ruminating (Pearce, 1965; Welch and Smith, 1968; Bae et al., 1979). Rumination activities such as rumination time, number of boli per day, and chewing rate are related to voluntary intake (Deswysen et al., 1987) and the amount of undigested feed residues remaining in the reticulo-rumen (Bae et al., 1979; McLeod and Smith, 1989).

Receptors in the reticulo-ruminal mucosa which respond to frictional stimulus and pressure are responsible for the initiation and control of rumination periods and intensity (Welch, 1982). Factors such as mastication, level of feeding, physical form of diet, or inert particles affect rumination time and frequency (Freer et al., 1962; Welch and Smith, 1970). Also, the particle size of rumen digesta affects the tactile stimulus controlling rumination. Rumination has been artificially induced by rubbing plant material against the rumen and reticulum wall, and removal of coarse material by grinding has reduced rumination time and jaw movements per unit weight of feed (Rook and Campling, 1959; Reid, 1983).

Rumination is influenced by physical characteristics and chemical properties of the diet (Balch, 1971; Osuji et al., 1975; Fujihara, 1980, 1981, 1982; Fujihara and Nakao, 1982). A direct relationship has been found between time spent ruminating and NDF intake (Cammell and Osbourn, 1972; McLeod and Smith, 1989).

Rumination time is limited to a maximum of 10 h/d (Bae et al., 1979; Kennedy, 1983), so the intake of intact large forage particles will be determined by how efficiently any particular feed can be broken down by rumination (Welch, 1982). Under these conditions, estimations of DM turnover are useful in order to estimate efficiency, but some methodological limitations still exist to determine these values for different sources of forages. Some attempts have been made to estimate turnover with results varying from 1.92 (Ulyatt, 1983) to 1.15 (Chai et al., 1984; Kennedy, 1985) for lucerne hay and 1.54 for bromegrass hay (Chai et al., 1984).

About 70% of the large particles contained in the regurgitated bolus can be reduced in size by secondary mastication during rumination (Reid et al., 1979; Chai et al., 1984, 1988; Ulyatt, 1983; Kennedy, 1985). The effectiveness of the comminution process during rumination will be enhanced by rumen digestion, thus it has been demonstrated that fragility of digesta particles of temperate grasses was doubled after digestion in the rumen for 12 h (Chai et al., 1984).

Combined Microbial and Mechanical Action

There is an important collaborative action between microbial digestion, mechanical reduction in particle size and passage (Campling et al., 1962; Balch and Campling, 1965; Chai et al., 1988). These three processes determine the digestibility of feed in the rumen and retention time of undigested residues (Campling, 1966). Microbial digestion does not appear to be essential for the breakdown and removal of large particles from the rumen (McLeod, 1986). Completely indigestible material may pass from the rumen following structural breakdown during

rumination (Welch and Smith, 1977, 1978; Murphy et al., 1989).
Microbial digestion accounted for only 19% of particle size reduction
although the OM digestibility was almost 50% (Murphy and Nicolletti,
1984). Murphy and Nicolletti (1984) suggested that microbial activity,
although very effective in removing the digestible fraction of feed, has
little effect on the size of indigestible fraction.

Particle comminution through mastication during eating and
rumination not only reduced particle size, but also increased the
potential microbial digestion by physical disruption of plant tissue and
increase in surface area (Pond et al., 1982, 1984; Chai et al., 1984,
1988). Microbial digestion by removing parts of cell walls reduced the
resistance of digested plant tissues to mechanical reduction in size
during rumination (Akin and Amos, 1976; Ulyatt, 1983; Akin et al., 1983;
Ulyatt et al., 1986). Such a combined and synergistic effect is
supported by evidence that the proportion of large particles reduced per
rumination cycle increases with increased time of digestion in the rumen
(Chai et al., 1984, 1988).

Resistance and Plant Structure

The ease with which plant material can be broken down into small
particles depends on the histological structure of the forage plant
(Grenet, 1989). In leaves the longitudinal strength is mainly found in
the midrib. Between 90 to 95% of the longitudinal stiffness may be
accounted for by fibrous bundles (Vincent, 1982), although they
constitute only about 5% of the total cross-sectional area in temperate
grasses. Greenberg et al. (1989) questioned the procedures used in the
work of Vincent (1982), however, and concluded that even though the

proportion of sclerenchyma fibers is normally less than 5%, sclerenchyma still influences the stiffness of grass leaves. Greenberg et al. (1989) pointed out, however, the role of epidermal tissue as the mechanical element that absorbs stress during tensile strength tests. Most of the transverse strength can be accounted for by the cuticle (Vincent, 1982) depending on cuticle thickness. Difficulties in disrupting the integrity of the epidermis can increase the force required for particle comminution and limit the accessibility of structures to microorganisms during digestion.

In the last few years, much effort has been expended in development of numerical relationships between intake, digestibility, and ruminal and mastication physiology. Research in the field of plant anatomy and digestibility has now started to include some aspects of mechanical reaction to stress that can be related to prehension, mastication, resistance to comminution, and intake. Attempts to relate this new information to differences in forage quality and animal production, particularly in tropical areas where the temperature, humidity, rain and incidental light are more variable in their effect, can help to understand basic principles and generate recommendations to improve management and production systems.

CHAPTER III
SEASONAL EFFECTS ON YIELD AND CHEMICAL COMPOSITION OF
'PENSACOLA' BAHIAGRASS AND 'MOTT' DWARF ELEPHANTGRASS

Introduction

'Pensacola' bahiagrass (*Paspalum notatum* Flugge) is an important
warm-season perennial grass in the Southeastern United States. Annual
production of up to 870 kg/ha of beef live weight (LW) gain has been
reported. Average daily gains (ADG) of steers on Pensacola pastures
decline progressively through the summer, however, with weight losses
common during late summer and early fall (Prates et al., 1974;
Sollenberger et al., 1989).

Lower summer gains have been observed even when stocking rate was
adjusted to maintain a relatively constant herbage allowance over the
season, so it is unlikely that the decreases in gain during summer are
due to a lack of available forage (Sollenberger et al., 1989). The
summer slump in ADG has been partially explained by reduction in OM
digestibility and nitrogen (N) concentration (Pitman et al., 1984;
Sollenberger et al., 1988b) and by decreasing grass intake (Prates et
al., 1974).

'Mott' dwarf elephantgrass (*Pennisetum purpureum*, Schum.) is a
selection from the selfed progeny of 'Merkeron' elephantgrass and was
released as Tift N-75 germplasm by the USDA Coastal Plain Experiment

Station in 1986 (Sollenberger et al., 1988c). Once introduced in Florida, evaluation of its potential has demonstrated that it can support up to 1500 kg LW/(ha·d), an ADG of approximately 1.0 kg and total beef production of nearly 500 kg LW/(ha·yr). In contrast to Pensacola, Mott is able to support consistently high levels of ADG throughout the grazing season (Sollenberger et al., 1989).

Stage of physiological maturity is known to be influenced by environmental conditions which result in differences in growth and chemical composition of grasses. Temperature, light and soil moisture interact to affect quality of Pensacola (Henderson and Robinson, 1982a; 1982b), and the response to these factors in other grasses depends on the characteristics of their fiber, species and rainfall.

The objective of this experiment was to compare yield, canopy structure, chemical composition and OM digestibility of Pensacola and Mott when harvested at 3, 5 and 7 wk of regrowth in early summer (June) and during the period when the summer slump in Pensacola is normally observed (September).

Materials and Methods

Location

The experiment was conducted at the Forage Evaluation Field Laboratory (FEFL) of the Institute of Food and Agricultural Sciences, University of Florida, from May to September 1987. The FEFL is located 20 km northeast of Gainesville, Florida (30° N latitude). Experimental plots were located on Adamsville and Sparr sands which have low

fertility and low OM content, and are very well drained (USDA, 1982). The climate is subtropical and humid with an average annual precipitation of 1300 mm. Climatological records during the experiment are in Table 3.1.

Experimental Design and Plot Arrangement

A completely randomized design arranged as a split-split-plot in time was used. Experimental variables were two grass species (main plots; Pensacola and Mott), three ages of regrowth (subplots; 3, 5 and 7 wk), and two cutting seasons (sub-subplots; June and September). Sources of variation, degrees of freedom, and error terms used are shown in Table 3.2. Statistical analyses were conducted by the General Linear Model (GLM) Procedure of the Statistical Analysis System (SAS, 1986). When three-way interactions (grass x age x season) existed (P<.11), data were analyzed by grass as a randomized block design arranged as a split-plot experiment where season was the main plot and age the sub-plot (Table 3.3). When age affected or interacted with any of the other effects (P<.11), trends in yield and chemical composition throughout the regrowth period were analyzed by polynomial contrasts). The PDIFF option of GLM was used to compare means when a two-way interaction existed.

Within separate established areas of Pensacola and Mott, three 55-m^2 blocks were selected. Each block was divided into three 15-m^2 (3*5 m) plots separated by 1-m alleys. The three age treatments were randomly assigned to plots within blocks. Plots were staged by clipping to a 5- (Pensacola) or 10-cm (Mott) stubble height at 1-wk intervals

Table 3.1. Climatological data recorded at the FEFL[a] in 5-day periods
            during the growth of Pensacola and Mott grasses in the
            experimental plots and hay field

Month	Days	Temperature[b] min.	max.	Rain-fall (mm)	Month	Days	Temperature min.	max.	Rain-fall (mm)
May	12-16	18	30	27.9	July/ Aug.	28-01	21	36	0.0
	17-21	18	31	5.5	Aug.	02-06	22	33	89.4
	22-26	16	31	34.2		07-11	22	37	1.0
	27-31	12	30	8.1		12-16	22	36	36.0
June	01-05	17	34	2.7		17-21	22	34	12.1
	06-10	14	33	4.8		22-26	19	36	0.0
	11-15	17	34	2.2		27-31	21	36	0.5
	16-20	19	36	1.5	Sept.	01-05	21	34	15.4
	21-25	20	36	7.8		06-10	19	34	4.3
	26-30	21	34	27.6		11-15	20	34	28.4

[a] Forage Evaluation Field Laboratory, Univ. of Florida.
[b] Degrees Celsius.

Table 3.2. Sources of variation, degrees of freedom, and
error terms for the analysis of variance

Source	df	Error term
Grass, G	1	B(G)
Block(Grass), B(G)	4	--
Age, A	2	A * B(G)
A * G	2	A * B(G)
A * B(G)	8	--
Season, S	1	S * B(G)
S * G	1	S * B(G)
S * B(G)	4	--
S * A	2	Residual
S * A * G	2	Residual
Residual	8	

Table 3.3. Sources of variation, degrees of freedom, and
            error terms for the analysis of variance by
            grass

Source	df	Error term
Block, B	2	--
Season, S	1	S * B
S * B	2	--
Age, A	2	Residual
A * B	4	--
A * S	2	Residual
Residual	4	

using a staggered schedule (Table 3.4). By staggering both staging and sampling dates, the mid-period of regrowth was the same for all age treatments.

On April 17, before the experiment started, plots received a routine maintenance application of 45, 39 and 74 kg/ha of N, phosphorus and potassium (K), respectively. At the staging in May, plots were fertilized with 30 and 60 kg/ha of sulfur and N. At staging in July and August, fertilization was the same as in May except for an additional application of 74 kg/ha of K. Irrigation was applied to the experimental areas as needed in such quantities that precipitation plus irrigation was never less than 40 mm/wk. As a result, soil moisture was not a limiting factor for grass growth in either season.

Sampling and Sample Processing

Sampling was performed at scheduled times (Table 3.4) in June and September. Due to differences between grasses in canopy structure and ground coverage, two 0.25-m^2 areas were clipped at a 5-cm stubble height in Pensacola plots and two 1-m^2 areas were clipped at a 10-cm stubble height in Mott plots.

Samples were separated manually into leaf blades and remainder (true stem, leaf sheath and the peduncle). Both fractions were dried at 60°C for 72 h, equilibrated with ambient humidity (air dry), weighed, ground to pass a 1-mm screen in a Wiley mill, and subsampled for subsequent laboratory analyses.

Table 3.4. Staging and sampling dates of Pensacola and Mott plots in
            June and September 1987

Season	Age(wk)	Staging	Sampling
June	3	May 26	June 16
	5	May 19	June 23
	7	May 12	June 30
September	3	Aug. 11	Sep. 1
	5	Aug. 4	Sep. 8
	7	Jul. 28	Sep. 15

Laboratory Analyses

Dry matter (DM) was determined by drying overnight at 105°C and OM by ashing for 16 h at 550°C. Determination of N was performed by the modified aluminum block digestion procedure of Gallaher et al. (1975), and ammonia in the digestate was determined by semiautomated colorimetry (Hambleton, 1977). In vitro OM disappearance was assessed by a modification of the two-stage technique (Moore and Mott, 1974). Leaf blade fractions were analyzed for acid-detergent permanganate-soluble lignin (LIG) and cellulose by the Goering and Van Soest procedures (1970), and ash-free neutral-detergent fiber (NDF) by a modified method described by Golding et al. (1985). Total DM yield (DM_y) was calculated as air dry weights times DM (determined at 105°C). Determinations of NDF, cellulose and LIG were made on the leaf fraction to monitor changes in cell-wall structure during the growing periods tested in the experiment.

Results and Discussion

Sources of variation, degrees of freedom, and mean square values are presented in Tables A3.1 to A3.3. There was a three-way (grass x age x season) interaction for DM_y (P=.0210) and IVOMD in leaf blade (P=.0003) and total canopy (P=.0001). For this reason a separate statistical analysis of the effect of season, age, and their interaction on these variables was conducted for each grass (Table 3.3). Proportion of leaf in the canopy, N concentration, and concentration of different

NDF fractions in the leaf blades were analyzed with the complete model (Table 3.2).

<u>Dry Matter Yield</u>

Dry matter yield was affected by an age x season interaction for Pensacola (P=.0042) and Mott (P=.0201; Table 3.5). Dry matter yield for Pensacola in June (P=.0001) and September (P=.0009) increased linearly from 3 to 7 wk. For Mott plots, the increase in DM_y was also linear in both seasons (June, P=.0002; September, P=.0157).

For both grasses DM_y was higher in June than in September (Pensacola, P=.0007; Mott, P=.0096). For Pensacola, DM_y was different between seasons at all growth intervals (3 wk, P=.0163; 5 wk, P=.0005; 7 wk, P=.0001). For Mott, DM_y was similar in both seasons at 3 wk of regrowth, but higher in June at 5 (P=.0017) and 7 (P=.0020) wk.

Even though the comparison of DM_y between grasses was not performed, across ages it appeared that Pensacola (3.1 Mg/ha) produced more DM than Mott (2.3 Mg/ha) in June, but DM_y was similar for the grasses in September (1.6 Mg/ha). These results contrasted with those of Sollenberger and Jones (1989) who found that herbage accumulation of Mott was greater than that of Pensacola under grazing conditions.

Light and temperature conditions over an experimental period can have a marked effect on seasonal patterns of DM accumulation (Santana et al., 1982). According to Henderson and Robinson (1982a) larger DM_y values should have been expected in September because higher

Table 3.5. Yield of dry matter (Mg/ha) for Pensacola and Mott at three regrowth intervals in June and September

Season	Age			SEM[b]	P-value[a]		
	3wk	5wk	7wk		Season (S)	Age (A)	S*A
─── Pensacola ───							
June	1.7	3.1	4.6	.1	.0007	.0002	.0042
September	1.1	1.6	2.3				
	(.0163)[c]	(.0005)	(.0001)				
─── Mott ───							
June	1.2	2.6	3.2	.1	.0096	.0002	.0201
September	1.0	1.5	2.2				
	(.2164)	(.0017)	(.0020)				

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=3).
[c] Probability level for the difference between season means within age and grass.

temperatures and rainfall were recorded during this season.

Effectiveness of irrigation probably was greater at the beginning of the summer, however, when higher irradiance levels are attained due to less interference from clouds (McCloud and Hill, 1987). Henderson and Robinson (1982a) also found a positive response in DM_y in Pensacola as light intensity increased. Furthermore, availability of reserves may have been higher after a period of winter dormancy, promoting a faster rate of regrowth in June compared to the middle of the summer.

Canopy Structure

Percentage of leaf blade in the canopy DM was affected by a grass x season interaction (P=.0002; Table 3.6). In June, percentage of leaf blades for Pensacola (59.0%) was markedly lower (P=.0001) than for Mott (88.7%). In September, differences between grasses were smaller (P=.0765).

Pensacola produces a large number of inflorescences at the end of the spring after very active vegetative growth. Thus, most of the non-blade fraction separated in June was made up of the flowering culm or peduncle and was not vegetative stem. Boddorff and Ocumpaugh (1985) found that even at advanced maturity (10 wk) four dwarf napiergrass varieties had 68% leaf blade in the DM. Values of 72 and 60% were reported for 3- and 7-wk regrowth. Values of Boddorff and Ocumpaugh (1985) were lower than those observed in this experiment for Mott in both seasons and might be due to differences in the period of the year when their experiment was conducted. Leafiness is one of the most desirable characteristics of Mott compared with other tropical grasses,

Table 3.6. Percentage of leaf blade in canopy dry matter of Pensacola
and Mott harvested in June and September

	June		September			P-values[a]		
						Grass	Season	
Item	Pensacola	Mott	Pensacola	Mott	SEM[b]	(G)	(S)	G*S
Leaf %	59.0	88.7	89.4	92.6	.97	.0009	.0001	.0002
	(.0001)[c]		(.0765)					

[a] Probability level for main effects and interaction.

[b] Standard error of means (n=9).

[c] Probability level for differences between grasses within season.

which become more stemmy with maturity, thus reducing their quality at a relatively early stage of regrowth.

In Vitro OM Disappearance

Total canopy IVOMD data are presented rather than leaf blade IVOMD because even though leaf blade was only 59% of Pensacola DM in June, leaf blade IVOMD was similar to that of remainder IVOMD. In vitro OM digestibility of total canopy was affected by a three factor interaction (P=.0001). Analysis by grass showed that a season x age interaction markedly affected total canopy IVOMD of both grasses (Pensacola, P=.0042; Mott, P=.0094; Table 3.7). For Pensacola, IVOMD decreased linearly (P=.0013) in June from 3 to 7 wk. In September, the effect of maturity on IVOMD was non-linear (P=.0160). In both seasons the reduction in IVOMD for Mott was non-linear (June, P=.0711; September, P=.0404).

Contrary to results normally observed in field experiments (Sollenberger et al., 1988b, 1989), IVOMD of 3- (P=.0003) and 7- (P=.0240) wk Pensacola regrowth in September was higher than that in June, and similar in both seasons at 5 wk of regrowth. These observations do not support the idea that the summer slump is related to a reduction in nutritive value of the grass. Perhaps the decline in animal performance during the summer slump is more closely related to changes in intake rather than to changes in digestibility of herbage in the pasture. It must also be considered that herbage character in clipped swards may differ from that in grazed pasture.

Table 3.7. In vitro organic matter disappearance (%) for the whole
            canopy of Pensacola and Mott at three regrowth intervals in
            June and September

| | Age | | | | P-value[a] | | |
Season	3wk	5wk	7wk	SEM[b]	Season (S)	Age (A)	S*A
	———— Pensacola ————						
June	48.9	47.5	43.5	.50	.0221	.0003	.0042
September	55.6	46.7	45.5				
	(.0003)[c]	(.1136)	(.0240)				
	———— Mott ————						
June	68.8	62.2	58.3	.34	.1286	.0001	.0094
September	69.5	65.1	57.0				
	(.2841)	(.0023)	(.1408)				

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=3).
[c] Probability level for the difference between season means within age
    and grass.

As has been observed for most tropical grasses (Minson, 1981; Castillo-Gallegos, 1983), age of regrowth reduced IVOMD. For Pensacola, the reduction was from 52.2 to 44.5% and for Mott from 69.2 to 57.6% from 3 to 7 wk. It seems that the effect of maturity was more severe for Mott than for Pensacola. This agrees with Minson (1981) who observed that the higher the initial value of IVOMD the higher the rate of reduction in digestibility through the time of regrowth, but Boddorff and Ocumpaugh (1985) observed very slow declines in nutritive value of Mott with increasing maturity.

Nitrogen Concentration

Nitrogen concentration in the total canopy was not affected by season but was affected by a grass x age interaction (P=.0031; Table 3.8). Maturity negatively affected N concentration of both grasses, but its effect was more severe in Mott (43% reduction from 3 to 7 wk) than in Pensacola (30% reduction). For Pensacola, effect of maturity was linear (P=.0003), but it was non-linear for Mott (P=.0670). Reductions in N concentration have been observed with increased maturity for both temperate and tropical grasses (Minson, 1981).

Mott had higher N concentration than did Pensacola at all age intervals (3 wk, P=.0020; 5 wk, P=.0012; 7 wk, P=.0059). Values in this experiment agree with those previously reported for Pensacola (Prates et al., 1974) and for Mott (Boddorff and Ocumpaugh, 1985; Sollenberger et al., 1988b). All values were over the minimum (1.12% N) required to maintain normal function of microorganisms in the rumen and to have

Table 3.8. Nitrogen concentration (% of dry matter) in the whole canopy of Pensacola and Mott at three regrowth intervals

	Age				P-value[a]		
Grass	3wk	5wk	7wk	SEM[b]	Grass (G)	Age (A)	G*A
Pensacola	2.0	1.6	1.4	.1	.0002	.0001	.0031
Mott	3.0	2.1	1.7				
	(.0020)[c]	(.0012)	(.0059)				

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=6).
[c] Probability level for the difference between grass means within age.

no limiting effect on intake (Milford and Minson, 1965; Minson and Milford, 1967).

Fiber Concentrations

There were no seasonal effects upon NDF, lignin, and cellulose concentrations. Ash-free neutral-detergent fiber was affected by a grass x age interaction (P=.0001; Table 3.9). Ash-free neutral-detergent fiber concentration in Pensacola was not affected by maturity, but in Mott maturity effect was non-linear (P=.0034) increasing the NDF concentration from 65.9 to 73.1%. Concentrations were higher in Pensacola than in Mott at all three age intervals (3 wk, P=.0001; 5 wk, P=.0002; 7 wk, P=.0002). Increased NDF due to maturation is a normal phenomena in grasses, mainly due to the thickening of plant cell walls with aging (Minson, 1981).

Changes in lignification due to maturity were not the same for both grasses (Table 3.9). In Mott leaves, maturity had a non-linear (P=.022) effect on lignin concentration. For Pensacola the lignin concentration did not change with maturity. Lignin represented 5.8 and 5.6% of the NDF in Pensacola and Mott, respectively, and 11.5 and 10.7% of the ligno-cellulose fraction (acid-detergent fiber).

There was also a grass x season interaction (P=.0465) for lignin concentration (Table 3.10). In both seasons lignin concentration was higher for Pensacola than for Mott (June, P=.0005; September, P=.0032). According to Wilson and Minson (1980), higher temperatures in September should have induced higher concentrations of lignin relative to June. It has been demonstrated (Henderson and Robinson, 1982a, 1982b), however, that the negative effect of temperature can be mediated by

Table 3.9. Ash-free neutral-detergent fiber, lignin and cellulose
concentrations (% of organic matter) in Pensacola and
Mott leaf blades at three regrowth intervals

	Age				P-value[a]		
Grass	3wk	5wk	7wk	SEM[b]	Grass (G)	Age (A)	G*A
─── Neutral-detergent fiber ───							
Pensacola	78.8	78.4	78.5	.35	.0001	.0001	.0001
Mott	65.9	72.3	73.1				
	(.0001)[c]	(.0002)	(.0002)				
─────── Lignin ───────							
Pensacola	4.4	4.6	4.6	.10	.0119	.0034	.0363
Mott	3.5	4.3	4.1				
	(.0014)	(.2617)	(.0642)				
─────── Cellulose ───────							
Pensacola	34.8	34.4	35.5	.13	.0026	.0001	.0001
Mott	30.8	33.7	34.4				
	(.0004)	(.0461)	(.0602)				

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=6).
[c] Probability level for the difference between grass means
within age.

Table 3.10. Lignin concentration (% of organic matter) in Pensacola and
Mott leaf blades harvested in June and September

	June		September			P-values[a]		
							Grass Season	
Item	Pensacola	Mott	Pensacola	Mott	SEM[b]	(G)	(S)	G*S
Leaf lignin	4.96	4.26	4.08	3.66	.05	.0119	.0001	.0465
	(.0005)[c]		(.0032)					

[a] Probability level for main effects and interaction.

[b] Standard error of means (n=9).

[c] Probability level for differences between grasses within season.

light intensity. More cloudy skies by the end of summer could have reduced the synthesis of phenolic compounds contributing to a trend toward higher digestibility of Pensacola in September than in June.

Cellulose concentration (table 3.9) was higher in Pensacola than in Mott at all growth intervals (3 wk, P=.0004; 5 wk, P=.0461; 7 wk, P=.0602). It increased with maturity in both grasses, but at a faster rate in Mott.

It can be concluded that growing season affected DM_y in both grasses. Higher availability of incidental light at the beginning of the summer likely stimulated higher rates of regrowth in June which accounted for the difference in DM_y between the two seasons. Different flowering characteristics of Pensacola changed its canopy structure. Inflorescence culms and seed heads accounted for 40% of DM_y in Pensacola grown on June. Mott had higher IVOMD and N, and lower NDF and lignin concentrations than did Pensacola across seasons and ages. The concentration and composition of cell wall in these two grasses was similar to that of most tropical grasses (Minson, 1981), but lower NDF and lignin concentrations in Mott suggested a better quality potential compared to Pensacola. Even though both grasses were sensitive to maturity, the decline in IVOMD and N was more severe in Mott than it was in Pensacola. However, IVOMD at the most advanced stages of regrowth in Mott was always higher than that observed in the youngest stages of Pensacola. Pensacola had a higher average IVOMD in September than in June but maturity reduced its nutritive value faster by the end of the summer. These data suggest that the summer slump in ADG observed in Pensacola by the end of the summer may not be explained solely on the

basis of seasonal differences in nutritive value. Effects of season on intake should be quantified.

Summary

A field plot experiment was conducted to determine the effect of growing season (June, J; September, S) and age of regrowth (3, 5 and 7 wk) on dry matter yield (DM_y), chemical composition and in vitro organic matter digestibility (IVOMD) of 'Pensacola' bahiagrass (*Paspalum notatum* Flugge) and 'Mott' dwarf elephantgrass (*Pennisetum purpureum* Schum.). Experimental plots were allocated in Adamsville and Sparr sands and fertilized with 165, 39, 158 and 60 kg/ha of N, P, K and S, respectively. The DM_y was affected by an age x season interaction in both grasses. It increased linearly in both seasons, but rate of increase was higher in J. The DM_y was higher for both grasses in J than in S and higher for Pensacola than for Mott in J. Percentage of leaf blades in the canopy DM of Pensacola in J was lower (60%) than in Mott (89%). Maturity reduced IVOMD and N concentrations linearly. Effect of maturity was more severe in S than in J for Pensacola. Mott IVOMD was more drastically affected by maturity than was Pensacola IVOMD, especially in J. Maturity affected N in Mott more than in Pensacola, but season did not affect N concentration. Total NDF and lignin concentrations varied with maturity depending upon grass species. Maturity increased NDF and lignin concentrations in Mott but did not have any effect in Pensacola, which had higher concentrations of both chemical components compared to Mott at all ages of regrowth. It is

concluded that superiority of Mott in forage quality can be explained partially by higher IVOMD and N and lower NDF and lignin concentrations compared to Pensacola. It is suggested that summer slump in ADG when cattle graze Pensacola cannot be explained totally by seasonal differences in nutritive value and that differences in intake should be determined.

CHAPTER IV
SEASONAL EFFECT ON THE PHYSICO-CHEMICAL CHARACTERISTICS OF RUMEN
CONTENT AND MASTICATION PATTERNS OF SHEEP FED 5-WEEK REGROWTH
'PENSACOLA' BAHIAGRASS AND 'MOTT' DWARF ELEPHANTGRASS

Introduction

Seasonal changes in animal performance observed in steers grazing
'Pensacola' bahiagrass (*Paspalum notatum* Flugge) can be explained by
changes in organic matter (OM) digestibility, nitrogen (N) concentration
(Sollenberger et al., 1988a) and intake (Prates et al., 1974). 'Mott'
dwarf elephantgrass (*Pennisetum purpureum* Schum.) is a high-quality
forage released recently in Florida, which is less susceptible to
seasonal differences, maintaining high levels of animal performance
throughout the grazing season (Sollenberger and Jones, 1989).

Ruminants cannot always adjust intake to meet their energy
requirements because many feeds are low in readily available nutrients.
In such cases intake is limited by gut fill or distension rather than by
caloric demands (Fisher et al., 1987). Changes in digesta transactions
in the reticulo-rumen (RR) are of particular significance in the context
of voluntary intake regulation. Increases in intake are accompanied by
an increased rate of removal of digesta OM from the RR (Campling, 1970).
Two mechanisms for removal exist: absorption, which depends on

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digestion, and passage of undigested OM to the omasum. The latter is dependent on RR motility and the degree of fineness of digesta (Poppi et al., 1980), and is affected by mastication and digestion.

In sheep, few particles over 1.2 mm in size are able to pass to the lower digestive tract, irrespective of diet type and level of intake (Poppi et al., 1980; Poppi et al., 1981; Ulyatt et al., 1986). Thus, the rate of particle size reduction may be a dominant factor regulating intake and the passage of fiber out of the rumen. Mastication during eating and rumination are the major contributors to the comminution of large particles (McLeod and Minson, 1988), but the efficiency in particle size reduction of these two processes depends on the resistance of plant tissues to breakdown and the amount of fibers present in these tissues (McLeod and Smith, 1989).

This experiment was designed to study the effect of season (June or September) and grass species (Pensacola or Mott) on efficiency of mastication and nutrient turnover in the rumen digesta of sheep. Both grasses were harvested at the same age of regrowth and offered at the same level of ash-free neutral-detergent fiber (NDF) intake on a metabolic weight basis, for 4 h daily.

Materials and Methods

Hay Preparation

Hays were produced at the Forage Evaluation Field Laboratory (FEFL) of the Agronomy Department, Institute of Food and Agricultural Sciences, University of Florida (30°N latitude). Soils were Adamsville

and Sparr sands which have low OM content, low fertility and are very
well drained (USDA, 1982), and the climate is subtropical and humid.
Climatological data during the growing season are in Table 3.1.

Approximately 0.5 ha of well-established swards of Pensacola and
Mott were harvested after 5 wk of regrowth in two seasons (June and
September) according to the schedule presented in Table 4.1. Initial
routine fertilization in April with 45, 39 and 74 kg/ha of N, P and K,
respectively, was followed by 34 kg of S and 67 kg of N/ha at staging in
May. In July the same amounts of S and N were applied plus 74 kg/ha of
K. Areas were irrigated as needed to provide the equivalent of 40 mm/wk
of total precipitation. The two grasses were harvested in both seasons
at 5- (Pensacola) or 10-cm (Mott) stubble height with a flail type
forage chopper, artificially dried at 60°C in a perforated-floor wagon,
placed in loose-weave plastic feed bags and stored in a barn loft. Hays
were fed without further preparation.

Experimental Design and Sample Collection

A 2x2 factorial arrangement of treatments in a 4x4 Latin square
design was used to determine effects of harvest season (June or
September) and grass (Pensacola or Mott) on physiological responses of
sheep. Treatment combinations will be identified hereafter as PJ, MJ,
PS and MS for Pensacola (P) and Mott (M) harvested in June (J) and
September (S).

Four mature crossbred sheep (44.5 ± 3.9 kg) fitted with permanent
rumen fistulas and housed in individual metabolism crates were fed the
four hays in four consecutive 18-d periods. Free access to a complete
mineral mixture and water was provided. Sheep were fed hay for

Table 4.1. Staging and harvesting dates, in two different seasons, for
5-wk regrowth Pensacola and Mott hays to be used in feeding
trials

Season	Grass	Staging	Harvesting
June	Pensacola	May 19	June 16
	Mott	May 26	June 23
September	Pensacola	Aug. 10	Sep. 14
	Mott	Aug. 3	Sep. 7

only 4 h daily (0800 to 1200 h). During the first 10 d, animals were offered more hay than they would consume in 4 h. Ash-free NDF intake was estimated by the analysis of NDF concentration in offered hay and orts. For the remaining 8 d, the quantity of hay offered was restricted so that each sheep was offered the same amount of NDF, on a metabolic body weight basis ($BW^{.75}$). Orts were taken after 4 h as before. After 3 d of adjustment to restricted intake, rumen samples were collected and physiological information was recorded for the next 5 d.

Total rumen and reticulum contents were removed manually twice: once on d 14 at 1200 h, immediately after the 4-h feeding period (post-feeding), and the other on day 18 at 0800 h, before hay was offered (pre-feeding). Rumen and reticulum contents were weighed, mixed, sampled, and returned to the rumen. Removal and sampling took no more than 20 min per animal. Three samples were taken in duplicate: (1) about 10 g were dried at 105°C for 48 h and ashed overnight at 550°C to determine total dry matter (DM) and OM concentrations; (2) 50 g were partially dried at 60°C for 48 h, ground to 1 mm and used for the determination of ash-free NDF (Golding et al., 1985) and indigestible NDF (residual NDF recovered after 144 h of in vitro digestion with a mixture of 1 part rumen fluid and 4 parts McDougall's artificial saliva; McDougall, 1948) and (3) approximately 250 g were frozen immediately at -4°C for determination of particle size distribution. An additional 250 g sample was collected at the pre-feeding sampling to prepare the Cr-mordanted small particles for mean retention time determination (Chapter V).

Mastication Patterns

An elastic band equipped with an electric micro-switch was fitted around the sheep's muzzle such that the switch was activated with every jaw movement. The switch was connected to an electronic counter which registered the total number of jaw movements during eating and rumination. Duplicate counts during the 4-h feeding period were made for each experimental period on d 14 and 16, and expressed as number per g of OM and NDF consumed.

On d 13, visual observations of rumination permitted number of jaw movements per regurgitated bolus to be counted. Time spent per bolus was recorded by means of a stop-watch. At least 100 rumination cycles were observed, and a mean rate of jaw movements (Jaw movements/second) during rumination was calculated. The mean rate was then used to convert the total number of jaw movements recorded during the 20 h between feeding to total time spent ruminating per day. The total time spent ruminating was recorded twice in a period (d 15 and 17) and expressed as min per g of OM and NDF consumed. Rumination during feeding periods was not observed

Particle Size Distribution

Samples were thawed, and the 250 g fresh sample (approximately 25 g DM) was refluxed with 1500 ml of neutral-detergent solution for 1 h and wet sieved through 1.18-, 0.6-, 0.3-, 0.15-, and 0.075-mm sieves. Fiber fractions were recovered on Whatman No. 541 filter paper, washed with distilled water and acetone, and dried at 60°C. Based on the critical particle size concept of Poppi et al. (1980), that fraction retained on the 1.18-mm screen was called "large particles" and the

other fractions pooled together were considered "small particles." Both
fractions were expressed as a percentage of the total NDF content in the
rumen.

Statistical Analyses

    The General Linear Model (GLM) Procedure of SAS (1986) was used
for the analyses of main effects of season and grass and their
interaction upon intake, mastication behavior and physico-chemical
characteristics of rumen content. Main effects and interactions were
considered to exist when P-value of parameter F was less than .11, and a
tendency was indicated by .11<P<.15. The sources of variation and
distribution of degrees of freedom for the analysis appear on Table 4.2.

    When a grass x season interaction existed, T-test (PDIFF option of
GLM, SAS) was used to determine the probability level of the difference
between season means within grasses or between grass means within
season. Mean squares are in Tables A4.1 to A4.8 and A4.10 to A4.12.

                          Results and Discussion

Hay Chemical Composition

    No differences between seasons of harvest were found in any of the
chemical components for either grass (Table 4.3). Dry matter
concentration was the same in both species, but Mott tended to have
lower concentrations of OM (88.4%) than did Pensacola (92.8%). The lower
OM may be the result of higher concentrations of minerals in plant
material or higher contamination with soil.

    Nitrogen was higher for Mott (2.4%) than for Pensacola (1.8%).
These values were equivalent to 15.3 and 11.2% crude protein (CP),

Table 4.2. Sources of variation and degrees of freedom for
the analysis of variance

Source	df
Period	3
Animal	3
Grass, G	1
Season, S	1
G * S	1
Residual	6

Table 4.3. Chemical composition of Pensacola and Mott hays harvested in June and September and used in animal trials

Item	Pensacola		Mott	
	June	Sept	June	Sept
Dry matter[a]	90.1	90.1	90.0	90.2
Organic matter[b]	92.9	92.8	87.3	89.4
Nitrogen[c]	1.6	2.0	2.6	2.3
Ash-free neutral-detergent fiber[c]	79.6	79.7	74.4	74.6
Ash-free acid-detergent fiber[c]	41.8	39.3	40.2	40.0
Lignin[c]	6.6	5.7	5.6	5.6
Hemi-cellulose[c]	37.8	40.4	34.2	34.7

[a] g/100g
[b] g/100g dry matter
[c] g/100g organic matter

respectively. According to the NRC (1985) 12% CP is required for growing animals, and according to Milford and Minson (1965) a minimum of 7% is necessary for normal microbial function in the rumen. Only PJ had a value below 12%, but none of the hays had less than 7% CP. Thus, a deficiency of CP may not be considered as an intake limiting factor for these grasses.

Pensacola and Mott had similar concentrations of ADF (40.6 and 40.1%), but Pensacola had a higher concentration of NDF (79.6%) than did Mott (74.5%); therefore, Pensacola had higher concentrations of hemicellulose (39.1 vs. 34.4%). With the exception of PJ, where the proportion of peduncle was 52% on a DM basis, all other hays had the same concentration of lignin. Lignin represented almost 15% of ADF.

Intake and Chewing During Eating

During adaptation, animals receiving PS consumed less OM and NDF than did those fed PJ or the Mott hays. Therefore, amount of hay offered to all animals during adjustment and collection was restricted to the level of NDF intake by sheep fed PS, on a metabolic body weight basis. No differences in NDF intake were observed among treatments because the amount of hay offered was restricted to provide equal NDF intakes. Differences (P=.0390) in OM intake between grasses were detected (Table 4.4), however, due to the higher NDF concentration in the OM of Pensacola compared to Mott (Table 4.3).

Ulyatt et al. (1986) reported that sheep fed indoors different kinds of hays ad libitum spend 200-400 min/d eating and that the length of the period was affected negatively by DM digestibility. McLeod and Smith (1989) found, however, that time spent eating per day in cattle

Table 4.4. Ash-free neutral-detergent fiber and organic matter intakes, and characteristics of mastication during eating by sheep fed Pensacola and Mott hays harvested in June and September

| | Pensacola | | Mott | | | P-values[a] | | |
| | | | | | | Grass Season | | |
Item	June	Sept	June	Sept	SEM[b]	(G)	(S)	G*S
Intake, g/kg BW:								
Ash-free neutral-detergent fiber (NDFI)	12.5	11.5	12.3	12.3	.45	.5305	.3127	.2959
Organic matter (OMI)	16.0	14.8	16.6	17.0	.55	.0390	.5131	.1774
Time eating, min	167	164	164	150	9.12	.3880	.3887	.5795
Intake Rate[c]	4.3	3.9	4.7	5.7	.5	.0749	.5506	.1924
Jaw movements:								
/min	101	94	110	107	2.3	.0022	.0766	.3913
/g OMI	25	25	25	20	1.5	.1817	.2044	.1962
/g NDFI	32	32	33	28	2.0	.6727	.2677	.2262

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=4).
[c] g OM/min.

did not change with source of forage. Even though animals in this experiment had free access to their daily allowance for 240 min/d, all of them ate for about 160 min (Table 4.4). During this period animals consumed 90 to 95% of the amount offered except for those receiving PS, who spent the same time eating but ate only 85 to 90% of that offered.

Intake rate was calculated as the quantity of OM consumed per min (Table 4.4). Mott was consumed at a higher (P=.0749) rate (5.2 g OM/min) than was Pensacola (4.1 g OM/min). Number of jaw movements per min (frequency) during eating was higher (P=.0022) when animals were offered Mott (109) than when they received Pensacola (97), and in both grasses frequency was higher for June harvest (P=.0766, Table 4.4).

Both intake rate and frequency measure the ease of making a bolus before swallowing during eating and are sensitive to changes in the structural characteristics of the grass. Ulyatt et al. (1986) suggested that diets resistant to breakdown by mastication can result in slower intake rates. They summarized unpublished data from Kennedy and Reid and presented a range of equivalent values from 4.1 (ryegrass) to 13.6 g DM/min (lucerne) for different types of forages. Differences observed among forages suggest the existence of anatomical (McLeod and Smith, 1989), physical and/or chemical (Lee and Pearce, 1984) differences, which to some extent predetermine their ease of comminution during chewing. Direct observations at the barn confirmed that animals consuming Mott made less effort per bite of grass before swallowing than did those fed the Pensacola hays. It can be suggested that under grazing conditions, these two attributes (rate of intake and frequency) can contribute to increased bite size and also biting rate, thus

increasing grass intake. On the other hand slower rates of intake and lower jaw movement frequencies (Pensacola vs. Mott) may increase the energy cost of eating per unit of DM consumed (Osuji et al., 1975), reducing the efficiency of utilization of grass energy.

Large variation in total number of jaw movements per day during eating was observed among hays (15000-17000), but no treatment effect was detected when number of jaw movements during eating was adjusted by OM or NDF intake (Table 4.4). Similar number of jaw movements per unit of NDF could indicate no differences in the structure of the fiber and this is supported by the small differences in chemical composition between grasses (Table 4.2). Both grasses had almost the same concentration of NDF, ADF and lignin, and lignin represented almost the same percentage in the ADF. Perhaps, rather than the absolute chemical concentration of cell walls, the tissue distribution of fibrous material in the leaf is a more important determinant of the effectiveness of mastication and deglutition, thus affecting intake rate.

Rumination

During rumination, no differences in total time spent ruminating were found among treatments (Table 4.5). Rumination time averaged about 320 min, which was less than the maximum of 600 min normally suggested (Dulphy et al., 1980) for sheep fed low-quality forages ad libitum. When rumination time was adjusted by OM or NDF intake, differences between grasses were detected. Animals receiving Mott remasticated about 100 min less per kg of OM (P=.0277) and NDF (P=.0785) than did those receiving Pensacola. There was no season effect and no interaction between grass and season.

Table 4.5. Characteristics of mastication during rumination by sheep
fed Pensacola and Mott hays harvested in June and September

Item	Pensacola		Mott		SEM[b]	P-values[a]		
						Grass (G)	Season (S)	G*S
	June	Sept	June	Sept				
Rumination time, min:								
/d	319	333	325	308	19.3	.6306	.9385	.4525
/kg OMI[c]	476	526	433	380	32.8	.0277	.9539	.1656
/kg NDFI[d]	608	676	584	525	41.2	.0785	.9063	.1740
Jaw movements, /bolus	52	60	50	48	3.6	.1047	.4052	.1703
Time/bolus, s	41.9	46.2	40.2	39.3	1.98	.0718	.4303	.2295
Frequency of chewing[e]	1.23	1.30	1.26	1.22	.04	.5333	.6426	.2436
Rumination Index[f]	80	96 (.0362)[g]	72	60 (.0874)	3.9	.0017	.6637	.0156

[a] Probability levels for main effects and interaction.
[b] Standard error of means (n=4).
[c] Organic matter intake.
[d] Ash-free neutral-detergent fiber intake.
[e] (Jaw movements/bolus) / (time/bolus).
[f] Number of jaw movements/100 g organic matter intake/kg BW.
[g] Probability level for differences between seasons within grass.

Rumination time has been positively related to fiber concentration in the hay and negatively related to digestibility (Welch and Smith, 1969). The restriction in NDF intake imposed by the experiment does not permit relating time spent ruminating to level of fiber intake, but differences between grasses in the time spent ruminating the same quantity of fiber reflect differences in structure that could be related to digestibility. As will be discussed later, differences in OM and NDF digestibility in vivo were observed between Pensacola and Mott, with higher values for Mott hays (Chapter V).

Even though total time spent ruminating per d was the same for all hays, there was a larger number (P=.1047) of jaw movements per regurgitated bolus for animals receiving Pensacola (56) compared to those receiving Mott (49). More jaw movements per bolus for Pensacola increased time spent per bolus, but frequency of chewing during rumination (jaw movements per second) did not differ among treatments. The mean frequency of 1.25 per second, corresponding to 75 jaw movements per min, agrees with that reported by Ulyatt (1983) who found no differences among a range of forages with different characteristics. As animals have the physiological capacity to perform a constant number of rumination jaw movements per unit of time, then differences in the number of jaw movements and time spent per bolus may be indicators of differences in chewing effort due to differences in physico-chemical characteristics of the grass (Lee and Pearce, 1984).

Rumination index (RI) is the number of jaw movements performed during rumination per 100 g of OM intake divided by the BW, and is an indicator of the mastication effort per unit of feed adjusted by animal

size. The adjustment for BW was done because differences in chewing efficiency were observed at different body sizes by Welch and Smith (1969) and Hooper and Welch (1983). Season of harvest markedly increased (P=.0362) RI for Pensacola in September compared to June and reduced that for Mott (P=.0874). Even though there was an interaction, values of RI for Pensacola (88.4) were much higher (P=.0017) than for Mott (66.0). Values found in this work for both grasses are within the equivalent range for legumes (63.3) and grasses (109.2) reported in other works in the literature on a DM basis (Fujihara, 1981; Fujihara and Nakao, 1982).

Particle Size Distribution in Rumen Digesta

There were no differences among treatments in the particle size distribution in the rumen content pre-feeding. The average for the four hays was 28.5 and 71.5% for large and small particles, respectively. At the post-feeding sampling the proportion of large particles was higher (P=.0036) for Mott (64.6%) than for Pensacola (60.8%) with no effect of season of harvest or interaction.

When the proportions of small and large particles were expressed as pools (g/kg BW), the difference between grasses in the proportion of large particles post-feeding disappeared (Table 4.6). Pre-feeding large-particle pools were affected by a grass x season interaction (P=.0572) with larger (P=.0369) values for PJ than for PS and no differences between Mott hays.

Small-particle pools post- (P=.0237) and pre-feeding (P=.0222) were higher for Pensacola, but were not affected by season of harvest (Table 4.6). However, a grass x season interaction tended (P=.1299) to

Table 4.6. Large and small ash-free neutral-detergent fiber particle
pools (g/kg body weight) in the rumen digesta of sheep fed
Pensacola and Mott hays harvested in June and September

| | Pensacola | | Mott | | | P-values[a] | | |
| | | | | | | Grass | Season | |
Item	June	Sept	June	Sept	SEM[b]	(G)	(S)	G*S
Large (>1.18 mm):								
Post-feeding	12.8	10.7	11.1	11.0	.69	.3384	.1489	.1806
Pre-feeding	3.8	2.4	2.0	2.3	.37	.0518	.2025	.0572
		(.0369)[c]		(.5404)				
Small (<1.18 mm):								
Post-feeding	8.4	6.8	5.8	6.1	.55	.0237	.3364	.1299
Pre-feeding	8.4	7.3	5.2	5.5	.83	.0222	.6638	.4332

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=4).
[c] Probability level for differences between seasons within grass.

affect the small-particle pools post-feeding with larger values (P=.0910) for PJ than for PS.

Classical methods to describe particle size distribution like Modulus of fineness, Mean particle size (Moseley, 1984), or Mean particle diameter (Cherney, 1989), in rumen digesta do not apply very well when the dynamics of particle size reduction and flow through the gastro-intestinal tract of ruminants are the main objectives of research. When this is the case, the concept of critical particle size and particle pools (Poppi et al., 1980) are the most appropriate.

Greater large-particle pools in the pre-feeding rumen digesta of Pensacola-fed animals indicate some inefficiency in particle size reduction during rumination. This inability could be related to the anatomical characteristics of the undigested residue. Larger number of jaw movements per bolus and longer periods of re-mastication per unit of OM or NDF intake, observed with Pensacola, support this suggestion.

For Pensacola hays the presence of greater large-particle pool in June at pre-feeding sampling, may be related to the higher proportion of stem fraction (peduncle) in the hay. Stem-like structures have more infiltration of fibers which have different spatial distribution compared to leaves, and that may increase their resistance to particle size reduction during rumination (Ulyatt, 1983; McLeod and Smith, 1989).

Finally, the amounts of small particles in the rumen digesta did not change from pre- to post-feeding for either grass. It can be speculated that the size of the small-particle pools is a constant foreach grass when intake is restricted, and that it is maintained through mastication patterns related to the physical and chemical

characteristics of the grass and rate constants of passage. In other words, the balance between production in, and passage from, the rumen of small particles tends to be zero in order to maintain a specific pool size characteristic of each forage. The fact that the small-particle pool pre-feeding was greater in animals fed Pensacola suggests the involvement of other physical conditions, like specific gravity (Ulyatt, 1983; Hooper and Welch, 1983; Murphy et al., 1989), as a critical factor determining the progress of the small particles through the reticulo-omasal orifice. Also, the greater large-particle pools could have affected the free flow of small particles by entrapping them in the fibrous mat (filter bed effect) (Welch, 1982; Van Soest 1982).

Effectiveness of Chewing in Particle Size Reduction

Effectiveness of chewing in particle size reduction during eating and rumination was estimated based on the post- and pre-feeding large-particle pools. For the estimation of the efficiency of particle size reduction during eating, three assumptions were made: (1) all consumed hay was in particles larger than 1.18 mm, (2) no particle larger than 1.18 mm had the ability to leave the rumen and (3) no rumination activity took place during eating. Thus, the difference between post- and pre-feeding large-particle pools represents the amount of hay particles that was ingested but resisted reduction in particle size by mastication during eating. Consequently, the difference between total hay consumed and that which resisted mastication, is the amount of ingested large particles that was reduced in size. Expressing the latter as percentage of ingested hay determines the efficiency of chewing during eating (%).

No differences in efficiency of mastication during eating were found among treatments. The overall mean of 27.8% (Table 4.7) agrees with that reported by Ulyatt et al. (1986) who found an average of 22.4% for sheep under different diets and 27.2% when fed leafy materials with morphological characteristics similar to the hays used in this experiment. Ulyatt (1983) and Ulyatt et al. (1986) established that animal variation in efficiency of chewing contributed to a reduction in differences among diets and also suggested that food is chewed, during eating, until some common end point in particle size structure is reached and then the bolus is swallowed. This concept has been validated by Fujihara (1981) and McLeod (1986).

Total number of boluses regurgitated per d was estimated by dividing the total time spent ruminating by the time spent per bolus. Unpublished data of John and Reid condensed by Ulyatt et al. (1986) indicates that about one third of the regurgitated digesta is effectively retained in the mouth for rechewing (remasticated bolus) and that it equals approximately 3.3 g DM/bolus, across different kinds of forages. Multiplying number of boluses by 3.3 and by NDF concentration in rumen digesta and adjusting the product for BW resulted in the quantity of regurgitated and remasticated NDF, which was expressed as g/(kg BW·d). No differences among treatments were found in remasticated NDF (Table 4.7).

Ash-free neutral-detergent fiber turnover expresses remasticated NDF as a multiple of NDF intake and indicates how many times the NDF fraction needs to be rechewed in order to achieve the physical characteristics required to leave the rumen. Turnover of NDF was higher

Table 4.7. Measurements of the efficiency of particle size reduction by
mastication during eating and rumination in sheep fed
Pensacola and Mott hays harvested in June and September

| | Pensacola | | Mott | | | P-values[b] | | |
| | | | | | | Grass | Season | |
Item	June	Sept	June	Sept	SEM[c]	(G)	(S)	G*S
Efficiency during eating, %[a]	27.2	28.5	26.1	29.3	5.48	.9753	.6925	.8641
Boluses, /d	454	436	479	466	38.6	.5052	.7142	.9454
Ash-free neutral-detergent fiber (NDF):								
Remasticated, g/(kg BW·d)	24.3	22.7	20.9	20.0	2.13	.1976	.5777	.8786
Turnover[d]	2.0	2.0	1.7	1.6	.2	.1017	.7811	.7339
Efficiency during rumination, %[e]	38.2	38.1	45.2	46.3	4.42	.1360	.9111	.8918
Specific fragility[f]	1.42	1.21	1.46	1.51	.09	.1047	.4052	.1703

[a] [Hay intake - (large particle pool post-feeding minus large particle
   pool pre-feeding)] / Hay intake.
[b] Probability level for main effects and interaction.
[c] Standard error of means (n=4).
[d] NDF remasticated / NDF intake.
[e] (large particle pool post-feeding minus large particle pool pre-
   feeding) / (number of bolus * 3.3 * % NDF in rumen digesta).
[f] g large particles that are reduced in size per chew, per 100 g of
   large particles remasticated.

(P=.1017) for Pensacola (2.0) than for Mott (1.6). No values have been reported for tropical grasses in the literature but the values of NDF turnover for Mott were similar to those reported for a range of temperate species (Ulyatt, 1983).

Finally, the efficiency of particle-size reduction during rumination is the amount of large particles reduced between meals (large-particle pool post-feeding minus large-particle pool pre-feeding) expressed as a proportion of the total NDF remasticated, adjusting both on a BW basis. The efficiency of rumination for particle size comminution tended to be higher (P=.1360) for Mott (45.8%) than for Pensacola (38.2%).

Efficiency of particle size reduction during rumination can be also quantified by means of the Specific Fragility (SF) index (Kennedy, 1985). It is the amount (g) of large particles that are reduced in size per chew, per 100 g of large particles retained in the mouth for remastication. Kennedy (1985) developed a highly significant linear relationship (r=-.99) between the number of jaw movements per bolus and SF. Thus, the Kennedy equation was used in this work to estimate SF for the four experimental hays. Specific fragility was higher (P=.1047) for Mott (1.48) than for Pensacola (1.32). Specific fragility reflects differences in the intrinsic characteristics of grass particles, which determine their resistance to be reduced in size by mastication during rumination. Rather than being related to the chemical composition or anatomical structure of the fed material, SF is related more likely to the process of selective microbial digestion, rate of digestion of

different tissues in the plant material, and structure of the residual
material after different periods of microbial attack.

Van Soest's hotel theory (Van Soest, 1982) applies to the concept
of SF. Microbial digestion progresses creating damage in the structure
of plant materials, particularly to the integrity of the cell walls, and
increasing the brittleness of the indigested residue. Anatomical
attributes limiting accessibility and susceptibility to microbial
digestion can remain in the residue absorbing the shearing stress of
teeth during mastication. According to Vincent (1982) and Greenberg et
al. (1989) the presence of large amounts of sclerenchyma fibers and
epidermal cells can absorb part of the force of mastication by
deformation before feed particles break into small pieces. Even more,
strong relationships between epidermis and vascular bundles through
sclerenchyma fibers can contribute to decrease SF.

Rumen Pools and Nutrient Mobilization

The rumen chemical composition was converted to absolute
quantities (g/kg BW) of the different components (pools) in order to
study the dynamics of rumen turnover (Table 4.8). Original data of
chemical composition appear in Table A4.9.

Differences in the magnitude of change in DM, OM and NDF pools
from pre- to post-feeding were found between grasses. During eating,
DM, OM and NDF pools increased in animals fed Mott more than in those
fed Pensacola hays. No differences were detected between grasses for
the increment in indigestible NDF pool from pre- to post-feeding.

Table 4.8. Dry matter (DM), organic matter (OM), ash-free neutral-detergent fiber (NDF) and indigestible NDF (INDF)[a] pools (g/kg BW) in the pre- and post-feeding rumen digesta of sheep fed Pensacola and Mott hays harvested in June and September

| | Pensacola | | Mott | | | P-values[b] | | |
| | | | | | | Grass | Season | |
Time	June	Sept	June	Sept	SEM[c]	(G)	(S)	G*S
			DM					
Pre-feeding	17.8	14.9	12.9	13.8	1.03	.0273	.3796	.1191
Post-feeding	29.8	25.3	26.5	26.9	1.32	.5395	.1756	.1224
			OM					
Pre-feeding	15.9	12.9 (.0828)[e]	10.6	11.5 (.5491)	1.00	.0162	.3436	.1034
Post-feeding	26.7	22.4	22.6	22.9	1.24	.2071	.1534	.1115
			NDF					
Pre-feeding	12.2	9.7 (.0745)	7.2	7.8 (.7544)	.83	.0061	.3144	.1074
Post-feeding	21.2	17.5 (.0311)	16.9	17.2 (.8323)	.94	.0449	.1178	.0764
			INDF					
Pre-feeding	9.6	8.0	6.1	6.6	.58	.0055	.3278	.1253
Post-feeding	12.3	10.0 (.0581)	8.3	8.7 (.6516)	.69	.0084	.2359	.0939

[a] NDF residue after 144 h of in vitro digestion.
[b] Probability level for main effects and interaction.
[c] Standard error of means (n=4).
[d] Probability level for differences between seasons within grass.

Pre- and post-feeding, all the rumen digesta components were (P<.11) or tended to be (.11<P<.15) affected by interactions between season and grass. There were differences between June and September only for Pensacola where the DM, OM, NDF and indigestible-NDF pools were or tended to be larger in June. No differences due to season effect were detected for Mott, either pre- or post-feeding. The DM (P=.0273) and OM (P=.0162) pools pre-feeding and total (P=.0061, pre-; P=.0449, post-) and indigestible (P=.0055, pre-; P=.0084, post-) NDF pools pre- and post-feeding were larger for Pensacola than for Mott hays. No differences in the size of DM and OM pools post-feeding were observed between grasses. Larger pre-feeding OM and NDF pools for PJ than for PS could have been related to the large proportion of peduncle present in the June hay, which could have slowed its rate of passage promoting larger accumulations of these two nutrients in the rumen digesta of PJ compared to PS.

Larger DM, OM, NDF, and indigestible-NDF pools in the pre-feeding rumen of animals fed Pensacola indicate a higher tendency of these animals to accumulate more residual material after a 20-h fasting period. Larger pre-feeding pools mean slower rates of disappearance either by fermentation or passage during rumination. Pre-feeding OM and NDF pools represented 99.4, 87.2, 63.8 and 67.6% of OM intakes, and 97.6, 84.3, 58.5 and 63.4% of NDF intakes for PJ, PS, MJ and MS, respectively. It is possible that under ad libitum feeding, factors contributing to these differences in ruminal pools can become important factors limiting intake. The disappearance of OM, NDF and indigestible NDF from rumen digesta during eating and rumination were calculated

(Table 4.9). Disappearance during eating was assumed to be the difference between the post-feeding pool and the sum of the pre-feeding pool plus the amount consumed during the 4-h feeding period. Disappearance during rumination was considered to be the difference between post- and pre-feeding pools. Disappearance occurs either by fermentation or by passage in the case of OM and NDF, and only by passage in the case of indigestible NDF. During eating, no differences among treatments were found with respect to OM and NDF disappearance, but more indigestible NDF disappeared in September for both grasses (P=.1063).

Reticulum motility varies with feeding behavior (Waghorn and Reid, 1983; Ulyatt et al., 1984; Waghorn et al., 1986). Frequency of contractions is 50% faster during eating than during rumination (1.0/min) and the amplitude of contraction is associated with changes in feeding activity and physical form of the diet (Okine et al., 1989; Reid, 1963). Thus, the amount of digesta that passed through the reticulo-omasal orifice would be expected to change within a day with higher values during eating. The larger amounts of large particles in the pre- and post-feeding rumen of animals receiving Pensacola (Table 4.6), and the larger proportions of residual total and indigestible NDF in the pre-feeding rumen digesta, could have increased rumen motility and could have been responsible for higher mobilization of indigestible NDF out of the rumen during eating.

During rumination and resting (20 h post-feeding) the difference between grasses was markedly increased with larger quantities of OM (P=.0788) and NDF (P=.1023) disappearing from the rumen of sheep fed

Table 4.9. Organic matter (OM), ash-free neutral-detergent fiber (NDF), and indigestible NDF (INDF)[a] disappearance (g/kg BW) from rumen digesta during eating and rumination in sheep fed Pensacola and Mott hays harvested in June and September

Item	Pensacola		Mott		SEM[c]	P-values[b]		
						Grass (G)	Season (S)	G*S
	June	Sept	June	Sept				
During eating:								
OM	5.1	5.3	4.6	5.6	.7	.8756	.4223	.5498
NDF	3.4	3.7	2.6	3.0	.6	.2677	.6394	.9066
INDF	.9	2.0	1.1	1.4	.4	.5338	.1063	.3178
During rumination:								
OM	10.8	9.4	12.0	11.4	.73	.0788	.2253	.6203
NDF	9.1	7.8	9.7	9.3	.6	.1023	.1963	.4579
INDF	2.7	2.1	2.1	2.2	.7	.7669	.6795	.6303

[a] NDF residue after 144 h of in vitro digestion.
[b] Probability levels for main effects and interaction.
[c] Standard error of means (n=4).

Mott. No differences were detected among hays in disappearance of indigestible NDF. When the quantity of disappeared indigestible NDF was expressed as a proportion of the total NDF disappearance, it was 53.3 and 29.0% for Pensacola and 33.9 and 22.9% for Mott, during eating and during rumination. These observations suggest that more NDF may leave the rumen by fermentation with Mott than with Pensacola, and conversely, more NDF leaves the rumen by passage with Pensacola.

Mott had higher frequencies of chewing and rates of intake during eating, which indicated less difficulty to form a bolus before swallowing, even though no differences in the number of jaw movements per kg of OM or NDF intake were detected. Differences in physical characteristics of forage could have been enhanced by microbial digestion. Different rates and extent of digestion of particular tissues may have rendered a more fibrous undigested residue in the case of Pensacola. This harder material required larger number of jaw movements per bolus and kg of OM (rumination index), and longer time spent ruminating per kg of OM and NDF intake compared to Mott.

Even though a larger number of jaw movements were required per bolus during rumination, a greater large-particle pool was found in the rumen digesta pre-feeding of Pensacola-fed animals. Also a greater small-particle pool was found, suggesting a process of small particles accumulation in the rumen possibly because of slower rate of passage. Efficiency of particle size reduction during eating and rumination did not differ among hays, but larger number of jaw movements per bolus and per kg of NDF to achieve the same degree of particle comminution in Pensacola, increased the energetic cost of mastication reducing the

efficiency of feed energy utilization compared to those animals receiving Mott. Less effective process of particle comminution and possible slower rate of passage of small particles out of the rumen in Pensacola-fed animals finally resulted in larger pools of OM, NDF and indigestible NDF in the pre-feeding rumen digesta. Disappearance of nutrients from the rumen during eating was similar for both grasses, but larger proportions of OM and NDF in post-feeding pools were removed either by fermentation or passage in animals fed Mott than in those receiving Pensacola hays. The pre-feeding NDF pool represented about 90% of NDF intake in Pensacola contrasting with 60% in the case of Mott. The differences between grasses in these proportions, and in frequency of chewing and rates of intake during eating, can become important determinants of the levels of voluntary intake of these two grasses under ad libitum conditions, affecting animal performance.

It is concluded that the differences in mastication patterns and rumen digesta composition observed between grasses in this experiment cannot be explained only by the differences in chemical composition of the hays. Therefore, it is suggested that marked differences between Mott and Pensacola could exist in the spatial distribution of the fibrous material inside their anatomical structure. This aspect was investigated in Chapter V.

Summary

Four ruminally-fistulated sheep were used in a 2x2 factorial arrangement of treatments in a 4x4 Latin square design to determine the effect of harvest season (June,J; September,S) and grass ('Pensacola' bahiagrass, *Paspalum notatum* Flugge; 'Mott' dwarf elephantgrass, *Pennisetum purpureum* Schum.) on physiological responses of sheep, when the access to hays was restricted to the same level of ash-free neutral-detergent fiber (NDF)/kg $BW^{.75}$ for 4 h daily. Rumen was emptied pre- and post-feeding and particle size distribution of rumen digesta was calculated after wet-sieving. Season affected frequency of chewing during eating with lower values in S for both grasses. Only for Pensacola was there an effect of season on rumination index (number of jaw movements/100 g OM intake/kg BW) and the size of the large-particle pool post-feeding, with larger values in S and J, respectively. Frequency of chewing and rate of intake during eating was higher for Mott than for Pensacola. Number of jaw movements, and time spent per regurgitated bolus and per kg of OM or NDF consumed during rumination were lower for Mott than for Pensacola but rumination index and NDF turnover were lower for Mott than for Pensacola. The small-particle pool was similar in pre- and post-feeding rumen digesta, and larger for Pensacola than for Mott. No differences in the amount of nutrients disappearing from the rumen during eating were detected among treatments, but larger quantities of OM and NDF disappeared from the rumen of Mott-fed animals between meals. It is suggested that possible differences in fiber spatial distribution rather than in fiber

concentration are the principal reason for the differences in mastication patterns, particle comminution, and pools of nutrients in the rumen digesta between these two grasses, and could explain expected differences in the level of intake in ad libitum feeding.

CHAPTER V

VOLUNTARY INTAKE, NUTRIENT DIGESTIBILITY, AND FLUID AND
PARTICULATE KINETICS IN SHEEP FED 5-WEEK REGROWTH PENSACOLA
BAHIAGRASS AND MOTT DWARF ELEPHANTGRASS

Introduction

When sheep were offered hays at the same level of ash-free
neutral-detergent fiber (NDF) intake in the experiment described in
Chapter IV, those consuming 'Mott' dwarf elephantgrass (*Pennisetum
purpureum* Schum.) had higher rate of organic matter (OM) intake prt and
frequency of chewing during eating than did those offered 'Pensacola'
bahiagrass (*Paspalum notatum* Flugge). Also, during rumination Mott-fed
animals had fewer jaw movements per bolus and spent less time ruminating
per kg of OM or NDF consumed. Eating rate (g OM/min) is highly
correlated with voluntary intake (Balch and Campling, 1962; Forbes et
al., 1972), and less effort during rumination may be related to a faster
and more extensive digestion process that possibly produces residues
which are less resistant to particle size reduction.

Relationships between anatomical structure of plant material and
its digestibility have been demonstrated (Ehlke and Casler, 1985; Akin,
1986; Wilson et al., 1989b). These relationships are based on the
accessibility of tissues to microbial colonization and on the higher
susceptibility of some tissues to microbial digestion (i.e., mesophyll)
compared to others (i.e., lignified vascular bundles). Wilson et al.

(1989b) found in tropical grasses strong linkages between epidermis and vascular bundles through the sclerenchyma fibers (girder structure). They suggested that the girder structure protects the epidermis from being shed and gives the digested plant material characteristics of stiffness that increase resistance to particle comminution. Epidermis and sclerenchyma fibers are the mechanical elements that determine the capacity of grass leaves to react by deformation rather than rupture in a stress-strain relationship caused by physical forces like those applied by teeth during mastication (Vincent, 1982; Greenberg et al., 1989).

In Chapter IV, pools of both large and small particles in the pre-feeding rumen digesta were greater for Pensacola than for Mott. A greater large-particle pool indicates higher resistance to particle comminution by rumination. A greater residual small-particle pool may be related to longer retention time of small particles in the rumen. Evidence exists (McClung, 1983; Waghorn et al., 1986) that the mean retention time (MRT) of rumen small particles is a critical determinant of voluntary intake; however, no information is available to support this hypothesis.

This experiment was conducted to determine (1) voluntary intake and nutrient digestibility of Pensacola and Mott harvested in June and September at 5 wk of regrowth; (2) the relationship between intake and passage kinetics of rumen small particles, entire hay and liquids, and (3) the effect of grass species and season of harvest upon anatomical characteristics of grass leaves. A further objective was to relate

changes in anatomical structure after digestion to voluntary intake and mastication patterns previously observed in Chapter IV.

Material and Methods

Hays and General Procedures

The four hays described in Chapter IV were used in a factorial arrangement of two species (Pensacola and Mott) and two seasons of harvest (June and September) in a completely randomized design. Twenty-four mature wethers crossbred of approximately 60-kg body weight (BW) were randomly allotted to individual metabolism pens and the four hays were randomly assigned to six pens each. Hays were offered ad libitum in amounts adequate to provide at 200-300 g orts/day. in Feces were collected in canvas bags attached to animals by a harness. The experiment consisted of a 14-d preliminary period during which sheep were adapted to the pens and hays, followed by two collection periods separated by a 4-d rest period. In collection period 1 (7 d) voluntary intake, digestibility and retention time of rumen small particles were measured. In collection period 2 (6 d) retention time of liquids and entire hay were quantified. In both collection periods the amount of hay offered, orts (refused hay), wastes (hay dropped on floor) and feces were measured. During the experiment animals had free access to water and a complete mineral mixture.

Before hays were harvested, four 1-m² representative samples from each field were collected and manually separated into leaf blade and remainder (stem, leaf sheath and inflorescence peduncle), dried at 60°C,

weighed, and ground through 1-mm screen. Sub-samples were dried at 105°C, and both fractions expressed as a percentage of total dry matter (DM).

Marker Preparation

Chromium-mordanted small particles

For collection period 1, pre-feeding rumen content samples were collected at the end of each period in the experiment described in Chapter IV and immediately frozen until they were processed to obtain the small-particle pool. Samples were thawed and approximately 250 g of fresh material (ca. 25 g DM) were refluxed with 1.5 l of neutral-detergent solution for 1 h and wet sieved through 1.18, 0.6, 0.3, 0.15 and 0.075 mm. Fractions retained on 0.3- to 0.075-mm sieves were pooled by hay (small particles), and treated with a 4% (w:v) $Na_2Cr_2O_7$ solution (12 ml per g of small particles) at 95°C for 24 h. The excess marker was reduced with 0.27 g of Ascorbic acid per g of small particles and, finally, the mordanted fiber was rinsed with distilled water and acetone (Cherney, 1989).

Chromium-mordanted hay

Approximately 300 g of entire hays were refluxed in fractions of approximately 40 - 50 g with neutral-detergent solution and mordanted with $Na_2Cr_2O_7$, as described above.

Cobalt-EDTA

Cobalt-EDTA (Uden et al., 1980) was prepared by treating 25.0 g Cobalt (II) Acetate with 29.2 g Ethylene Diamine Tetraacetic Acid (EDTA) in presence of 4.0 g NaOH for 24 h. The product was oxidized with 20 ml

of 30% (v:v) Hydrogen Peroxide, washed with 80% (v:v) Ethanol, filtered and dried at 100°C.

Marker Dosing and Feces Collection

Chromium-mordanted small particles were offered to the animals as a single dose before hay was fed on the first day of collection period 1. Five grams Cr-mordanted small particles were mixed with 17 g molasses and 40 g corn meal and placed in the feeder. Animals were allowed to consume the mixture for 0.5 h, and uneaten marker was recovered. Three animals did not consume enough; thus, the dose was suspended in distilled water and infused directly in the rumen through an esophageal tube.

At the beginning of collection period 2, 10 g of marked entire hay were offered as a single dose mixed with a small quantity of normal hay before the daily meal. Also, 190 mg of Cobalt (as EDTA salt) diluted in 10 ml of distilled water was dosed orally just after the Cr-mordanted hay was consumed.

In both collection periods, feces were removed from fecal collection bags 4, 8, 12, 16, 20, 24, 30, 36, 42, 48, 60, 72, 84, 96, 108, 120, 132 and 144 h after dosing the markers. An extra sample at 168 h was obtained in collection period 1 in order to complete the 7 d required for the intake and digestibility trial. Excretion time for each sample was recorded as the mean of the collection time and the previous collection time. At each time the total feces in the collection bag were weighed, mixed and sampled. A 20% representative sample was dried at 60°C for 48 h, equilibrated with atmospheric

humidity, and weighed. The dried samples were ground through a 1-mm
screen in a Wiley mill and stored for chemical analyses.

Marker Analysis and Passage Parameters Estimation

About 5 g of partially dried feces were dried at 105°C for 48 h
and ashed at 600°C for 3 h to determine DM and OM concentration. Ash
was treated with a mixture of 4% (w:v) Potassium Bromide and 3% (w:v)
Manganese Sulfate in Phosphoric acid, according to Williams et al.
(1962). The ash solution was made to volume (50 ml) with distilled
water and the concentrations of Cr and Co were determined by Atomic
Absorption Spectrophotometry (Perkin-Elmer, 1976). One and two
compartment, age dependent and age independent Gamma distribution models
(Pond et al., 1988) were solved for marker fecal excretion using the
Marquardt method of the Non-linear Model (NLIN) Procedure of SAS (1986).
Models were fit to marker concentration in feces over time. Lag and
fractional passage rate constants (k_1 and k_2) were estimated and used to
calculate MRT (MRT = Lag + $2/k_1$ + $1/k_2$). The mean square of the
residual and the asymptotic standard error (ASE) of the estimates were
the criteria used to judge fitness of the data to the model and validity
of parameter estimates. Only parameter estimates with ASEs less than
10% were accepted. Information from sheep 2 fed Mott harvested in
September is used to show the distribution of observed values over
adjusted model in Figure 5.1. Original data and statistics appear in
Table A5.1.
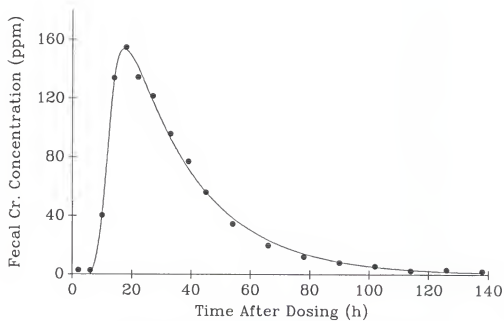
Figure 5.1. CHROMIUM FECAL EXCRETION BY SHEEP
DOSED Cr—MORDANTED SMALL PARTICLES

Voluntary Intake and Apparent Digestibility

Hays were offered once daily in amounts to provide approximately 200 g of orts per day. A representative and constant proportion of the daily offered hay was collected and pooled by pen and period (ca. 2 kg per animal). The total quantity of orts and wastes produced during the collection periods was dried at 60°C and then ground and sub-sampled. Hays, orts and wastes were ground initially through a 4-mm screen, and sub-samples (about 200 g) were reground through a 1-mm screen in a Wiley mill for subsequent analyses.

A composite fecal sample was prepared for each animal by sub-sampling 10% of the dry weight excreted at every sampling time during collection period 1. Offered hay, orts, waste and feces samples were then analyzed for DM, OM and NDF (Golding et al., 1985) concentrations, in order to calculate intakes, apparent digestibility coefficients and digestible fraction intakes of OM and NDF.

Anatomical Structure and In Vitro Tissue Digestion

Before the grasses were harvested for hay, approximately 1 kg of green, well-expanded leaf blades was hand-plucked and immediately stored at -20°C. Five-millimeter cross-sections were excised midway between tip and collar of 10 randomly selected blades, and embedded and frozen in O.C.T. Compound (Miles Scientific # 4583) in a cryostat set at -20°C. Transverse sections 16-micron thick were mounted on microscopy slides fitted with double-stick-tape (Scotch Cat.# 136) and fixed in 4% (v:v) Glutaraldehyde solution in Potassium Phosphate Monobasic Buffer (PBS). After 48 h, slides were rinsed in PBS and photomicrographs at 100x were taken under UV light with a Nikon fluorescence microscope. Negatives

were projected onto the tablet of a Hipad Digitizer (Houston Instruments) and the digitizing system (MicroComp Digital Image Analysis System; Southern Micro Instruments, Inc.) was used to trace and quantify the proportion of selected tissues (epidermis, sclerenchyma and vascular bundles). A portion of blade cross section between two (including one) major vascular bundles, approximately midway between the midrib and leaf margin, was selected to determine tissue areas, which were expressed as a percentage of the total examined area. Mesophyll was estimated by the difference between 100% and total percentage occupied by all other tissues.

Extra microscopy slides (from the same 10 leaves used for anatomical studies) were prepared as described before to examine the relative extent of tissue digestion. Slides with 16-micron cross sections were immersed in a 1:4 (v:v) mixture of rumen fluid and McDougall's artificial saliva (McDougall, 1948) under CO_2 and incubated at 39°C. After 24 h of in vitro digestion the sections were fixed and digitized as described above. As mesophyll was completely digested in both grasses the area of the different tissues was expressed as percentage of the total area occupied by non-digested epidermis, sclerenchyma and vascular tissues, using as reference the space between two (including one) major vascular bundles.

Rate Constant of Digestion

Duplicates of 1 g DM from each of the four hays were incubated at 39°C, in vitro, with a 1:4 (v:v) mixture of rumen fluid and McDougall's artificial saliva (McDougall, 1948). Digestion was interrupted after 3, 6, 9, 12, 18, 24, 36, 48, 60, 72, 96, 108, 120 and 144 h, and the

residue extracted with neutral-detergent solution in order to estimate the undigested NDF at each time, and the NDF indigestible fraction after 144 h. Rate constant of digestion was estimated by the model proposed by Fisher et al. (1989).

Statistical Analyses

General Linear Model (GLM) Procedure of the Statistical Analysis System (SAS, 1986) was used to investigate the effects of season, grass and their interaction with respect to intake and digestibility of nutrients, and passage kinetic parameters, according to the degrees of freedom distribution presented in Table 5.1. Main effects and interactions were considered to exist when the P-value of parameter F was less than .11, and tendencies were indicated by P-values ranging from .11 to .15. The mean squares are in Tables A5.2 to A5.4. The same statistical model was used for tissue distribution in leaf blades and digested residues; however, due to some losses during fixation and digestion, the GLM procedure was used to estimate least squares means for comparison of treatments with different number of observations. Analysis of variance with the appropriate distribution of degrees of freedom appear on Tables A5.6 and A5.7.

The PDIFF option of SAS was used to determine the probability level for the difference between season means within grasses and grass means within season when interactions existed. Correlation analyses (Pearson correlation coefficients) were performed between OM, NDF and digestible OM intakes, and nutrient digestibility coefficients and MRT.

Table 5.1.   Sources of variation and distribution of
degrees of freedom for the analysis of
variance of intake, digestibility and
passage kinetics

Source	df
Grass, G	1
Season, S	1
G * S	1
Error	20

Results and Discussion

Apparent Digestibility

A grass x season interaction was found for DM (P=.0612), OM (P=.0219) and NDF (P=.0009) digestibility coefficients (Table 5.2). The DM (P=.0104), OM (P=.0029) and NDF (P=.0009) digestibilities were higher for September than for June harvests for animals receiving Pensacola, but similar for both seasons in animals fed Mott. The digestibilities of DM, OM and NDF of Mott were higher (P<.005) than those of Pensacola in both seasons.

The superiority of Mott over Pensacola has been previously reported based on in vitro determinations on samples collected during different grazing experiments (Sollenberger et al., 1988a, 1988c, 1989, Sollenberger and Jones, 1989) and also in the plot experiment of this work reported in Chapter III. The difference in DM or OM digestibility between Pensacola and Mott seems to be more related to the differences in NDF digestibility (Table 5.2) rather than to differences in the NDF concentrations (79.6 vs 74.5%, Table 4.3). Parallel in vitro NDF digestion tests (Table 5.3) showed that about 76.5 and 85.2% of the potentially digestible NDF was digested after 48 h in Pensacola and Mott hays and that the indigestible OM after 144 h contained 28.1 and 18.6% of NDF. This corresponded to 35.5 and 25.2% of total NDF in the original samples, respectively. Digestibility of cell walls is affected not only by the degree of lignification but also by the chemical composition of lignin (Akin, 1989), thus differences in the

Table 5.2. Apparent digestibility coefficients (%) for sheep fed
Pensacola and Mott hays harvested in June and September

Item	Pensacola		Mott		SEM[b]	P-values[a]		
						Grass (G)	Season (S)	G*S
	June	Sept	June	Sept				
Dry matter	57.2	60.0	65.1	65.1	.71	.0001	.0578	.0612
		(.0104)[c]		(.9837)				
Organic matter	60.3	63.8	67.2	67.1	.73	.0001	.0317	.0219
		(.0029)		(.9014)				
Ash-free neutral-detergent fiber	63.5	68.1	73.7	71.8	.83	.0001	.1229	.0009
		(.0009)		(.1236)				

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=6).
[c] Probability level for differences between seasons within grass.

Table 5.3. Fractionation and measurements of in vitro digestion of the ash-free neutral-detergent fiber of Pensacola and Mott hays harvested in June and September (n=2)

Item	Pensacola		Mott	
	June	Sept	June	Sept
Ash-free neutral-detergent fiber, g/100 g OM:				
Total	79.1	79.0	74.3	73.5
Indigestible[a]	28.1	28.1	19.6	17.6
Potentially digestible (PDNDF)	51.0	50.9	54.7	55.9
PDNDF digested (%) at:				
24 h	32.5	36.0	50.0	37.0
48 h	76.1	76.9	87.7	82.8
96 h	92.3	95.6	96.3	94.6
Rate constant of digestion, /h	.025	.028	.032	.028

[a] Residue after 144 h of in vitro digestion.

concentration of Phenolic and p-Coumaric acids can determine differences in cell wall digestibility in plant materials with similar lignin concentration (Akin, 1982a, 1989). It is possible that differences in lignin chemical composition exist between Pensacola and Mott that could have affected differently the extent of NDF digestion in these two grasses.

Proportions of leaf blades in the DM averaged 89% except for Pensacola harvested in June, which had 48% due to the presence of seed heads and inflorescence culms. However, in vitro OM disappearance for leaf blade was 46.6% and for sheath plus stem was 45.0%, so the lower proportion of leaves does not explain fully the difference in digestibility observed between Pensacola's June and September harvests. Pensacola harvested in June had slightly higher lignin concentrations (Table 4.3).

Intake

Intakes of total and digestible OM were affected by grass and season (Table 5.4). Both total and digestible OM intakes were higher (P=.0161, P=.0003) for Mott (20.5 and 13.8 g/kg BW) than they were for Pensacola (17.8 and 11.0 g/kg BW), and higher (P=.0056, P=.0112) for June (20.8 and 13.3 g/kg BW) than for September (17.7 and 11.5 g/kg BW) harvests of both grasses.

Digestible OM intake is considered to be the best expression of forage quality because it indicates the quantity of energy available to the animal. Moore (1987) proposed the concept of Quality Index (QI), which expresses digestible OM intake as a multiple of the maintenance requirement. Thus, QI indicates how much digestible OM remains

Table 5.4. Total and digestible organic matter and ash-free neutral-
detergent fiber intakes (g/kg BW) by sheep fed Pensacola and
Mott hays harvested in June and September

Item	Pensacola June	Pensacola Sept	Mott June	Mott Sept	SEM[b]	Grass (G)	Season (S)	G*S
Organic matter:								
Total	19.9	15.7	21.7	19.4	1.04	.0161	.0056	.3904
Digestible	12.0	10.0	14.6	13.0	.64	.0003	.0112	.7718
Ash-free neutral-detergent fiber:								
Total	15.8	12.6	16.2	14.4	.84	.2112	.0076	.3826
Digestible	10.1	8.6	11.9	10.3	.56	.0039	.0121	.9523

(The P-values columns are under the heading "P-values[a]")

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=6).

Table 5.5. Quality index for Pensacola and Mott hays harvested in June
and September

Item	Pensacola		Mott		SEM[b]	P-values[a]		
						Grass (G)	Season (S)	G*S
	June	Sept	June	Sept				
Quality index	1.15	.95	1.41	1.24	.06	.0001	.0042	.7872

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=6).

available for production after the maintenance requirements have been met.

Maintenance requirement for growing sheep are equivalent to 29 g of digestible OM per kg of metabolic body weight ($BW^{.75}$) and this value was used as denominator to compute QI from digestible OM intake data generated in this experiment (Table 5.5). The QIs were different between grasses (P=.0001) and between seasons (P=.0042). Mott (1.32) consistently had higher values compared to Pensacola (1.05) and for bothgrasses QI was lower for the September harvests. The effect of season was extremely detrimental for Pensacola where the value of QI for September (0.95) was reduced to below maintenance. The differences in intake of digestible OM in this study suggests that intake may be more important than digestibility in determining the differences in forage quality between Pensacola and Mott. These data suggest that substantial reduction in intake may be the main factor responsible for the decline in animal performance frequently observed by the end of the summer (summer slump) in animals grazing Pensacola.

Ash-free neutral-detergent fiber intake was not affected by grass species but was lower (P=.0076) for September with both grasses (Table 5.4). Across treatments average NDF intake by sheep was 14.5 g/kg BW. This value was slightly higher than that found by Mertens (12.5 g/kg BW) with dairy cattle across different diets (cited by Cherney, 1989), but lower than the 18.0 g/kg BW found by Worrell (1982) for a range of tropical grasses across different regrowth intervals fed to sheep. Even though average NDF intake in this experiment was close to that reported by Mertens, the range of values found for these four hays was 12.6 to

16.2 g/kg BW. Cherney (1989) determined NDF intakes for grasses with uniform NDF concentration but different morphological structure, and suggested that it may not be possible to predict DM intake from NDF concentration as proposed by Mertens because NDF intake was not constant. Data in the present experiment support her conclusion.

Digestible NDF intake was higher (P=.0039) for Mott (11.1 g/kg BW) than for Pensacola (9.4 g/kg BW), and higher (P=.0121) for June (11.0 g/kg BW) than for September (9.5 g/kg BW). Even though there were differences in OM intake between Pensacola and Mott, the lower concentration of NDF in Mott OM equalized the NDF intake among hays. However, higher NDF digestibilities observed for Mott made the differences in digestible NDF intake again evident.

Passage Parameters

There were no differences among treatments with respect to lag period for rumen small particles, but the MRT tended (P=.1245) to be longer for Pensacola and was (P=.0824) longer for September with both grasses (Table 5.6). Small particles were collected from the rumen content before feeding. Even though they had already reached the critical size to progress through the reticulo-omasal orifice (1.18 mm; Poppi et al., 1980) they still remained in the rumen. Small particles may have stayed longer in the rumen either because they were trapped in the large-particle pool (bedding effect; Welch, 1982) or because their specific gravity was so great that they sank in the reticulum or the bottom of the ventral sac of the rumen. Small particles must have certain specific gravity characteristics in order to be passed to the omasum during reticulum contractions (Campling and Freer, 1962).

Table 5.6. Lag and mean retention times (MRT) for the rumen small
particles, liquid phase and entire hay in sheep fed
Pensacola and Mott hays harvested in June and September

	Pensacola		Mott			P-values[a]		
Item	June	Sept	June	Sept	SEM[b]	Grass (G)	Season (S)	G*S
Lag, h:								
Small	8.4	9.2	7.9	7.9	0.6	.1613	.5238	.5721
Liquids	8.3	9.2	8.3	8.5	0.4	.3812	.1885	.3850
Total tract MRT, h:								
Small	42.2	47.2	38.8	42.8	2.45	.1245	.0824	.8242
Liquids	17.9	18.7	17.8	18.6	0.49	.8014	.1192	.9157
Entire	59.0	57.9	54.5	55.6	2.76	.1203	.9714	.6907

[a] Probability level for main effects and interaction.
[b] Standard error of means (n=6).

In the experiment described in Chapter IV under restricted intake conditions, the small-particle pool represented about 65 and 43% of daily NDF intake in Pensacola and Mott, respectively. Under ad libitum conditions, like in this experiment, delays in the normal progress of small particles through the reticulo-rumen could increase the accumulation of small these particles in the rumen and create physical barriers for higher voluntary intakes. Using the information reported by McClung (1983) and Waghorn et al. (1986) it was estimated that the small-particle pool in the rumen pre-feeding is responsible for reductions in voluntary intake when bermudagrass and digitgrass (McClung, 1983) or early and late cuts of Italian ryegrass (Waghorn et al., 1986) were compared.

Fecal small particles extracted with neutral-detergent solution had shorter MRT (Cherney, 1989) than did the rumen small particles in this study. These results can be expected because particles that appear in the feces are those that already have passed through the reticulo-omasal orifice, so they have already met the requirements in terms of size, digestion and density to escape (Cherney, 1989). Small particles used in this study, however, were those which did not necessarily meet those requirements, except for the size.

No differences among hays were found in lag time and MRT of Co-EDTA, which was the marker used to trace the passage of the liquid phase through the gastro-intestinal tract (Table 5.6). Results of this study contrast with those of Poppi et al. (1981) and Lindberg (1985) who showed relationships between retention time of liquids and source and

level of intake of feeds, but are supported by the results of Cherney
(1989) who found no difference in the lag and MRT of Co-EDTA excretion
among different types of forage (with different morphological
structure), at two different levels of intake. However, values found in
this work are lower than those reported by Cherney (1989) who fed
temperate annual grasses.

Lag times of entire marked hay are not reported in Table 5.6
because of problems with the estimation of this parameter. Even though
there was a rest period of 4 d between collection periods 1 and 2, small
quantities of Cr were detected in the feces at the beginning of
collection period 2 (control collection at time 0). This Cr was
considered residual marker from the collection period 1 when Cr-
mordanted rumen small particles were dosed and its presence invalidated
the computation of lag for collection period 2.

No differences in the MRT of entire marked hay were detected among
treatments with a mean value of 57 h for the four hays (Table 5.6).
Recent studies (Robinson and Sniffen, 1983; Lirette and Milligan, 1989;
Taminga et al., 1989) indicate that the Cr-mordanting technique may not
be the most appropriate for tracing the passage of large particles in
the gastro-intestinal tract of ruminants. Neutral-detergent extracted
materials bound to Cr can release the metal during digestion and only
small particles retain the marker because of the strong hexacoordinate
ligands formed with hydroxyl groups during mordanting. Thus, Cr
excretion curves are not representative of long feed particles and may
underestimate their MRT. On the other hand, chewing by sheep can
eliminate to a large extent the difference in initial particle size and

brittleness of feed (Ulyatt, 1983), resulting in similar MRT among forages of different physical characteristics (Thomas and Campling, 1977).

Anatomical structure

The proportion of epidermal tissue in leaf blades was affected by a grass x season interaction (P=.0077; Table 5.7). Mott (32.7%) had a larger proportion of epidermis than did Pensacola (25.9%) in both seasons but the difference between grasses was greater in June than in September. Microscopic observations (Figure 5.2) showed that in addition to differences in proportion, there were differences in structure also. In Pensacola leaves, the epidermal cells had thicker walls and were more tightly arranged than in Mott leaves. Also, Pensacola had a thicker cuticle layer. Micrographs obtained with the Scanning Electron Microscope from surface view of the epidermal tissue showed that a tighter linkage between epidermal cells was present in the case of Pensacola, confirming the observations on similar samples under the light microscope (S.L. Russo, 1989; personal communication).

Pensacola (5.4%) had larger (P=.0001) proportions of sclerenchyma fibers than did Mott (1.6%; Table 5.7). While the distribution of sclerenchyma fibers in Pensacola leaves was along the cross sectional area and at the top and bottom of primary and secondary vascular bundles, sclerenchyma fibers in Mott were more concentrated at the top and bottom of principal vascular systems and in smaller bundles (Figure 5.2). The characteristic size and distribution of sclerenchyma fibers in Pensacola has been observed in other tropical species (Akin and Burdick, 1973; Wilson et al., 1989b) and has been

Table 5.7. Least squares means for the tissue distribution (%) in the cross section of 5-week Pensacola and Mott leaf blades harvested in June and September

Item	June Pens.	June Mott	September Pens.	September Mott	SEM[b]	Grass (G)	Season (S)	G*S
Epidermis	25.0	34.3 (.0001)[c]	26.8	31.2 (.0010)	.83	.0001	.4317	.0077
Sclerenchyma	5.1	1.7	5.7	1.4	.37	.0001	.4543	.2544
Vasc. bundle	20.5	21.9	20.6	18.5	1.09	.7865	.2339	.1235
Mesophyll	49.4	42.1 (.0006)	46.9	48.8 (.3160)	1.33	.0604	.1272	.0019

[a] Probability level for main effects and interaction.
[b] Standard error of means.
[c] Probability level for differences between grasses within season.

(A)

(B)

Figure 5.2. Micrographs (300x) of cross sectional area of (A)
Pensacola and (B) Mott leaf blades collected at 5
wk of regrowth in the hay fields.

called "girder" structure. The girder consists of firm linkages between the epidermis and the vascular bundles by means of highly lignified sclerenchyma fibers. Such structure protects the epidermis from being shed during mastication and offers significant resistance to microbial attachment and digestion (Wilson et al., 1989b). Vincent (1982) and Greenberg et al. (1989) have demonstrated that sclerenchyma and epidermal tissues are the more important determinants of the mechanical characteristics of leaf blades, being responsible for 90 to 95% of the longitudinal stiffness and strength (sclerenchyma fibers) and for the load-bearing function (epidermis) under stress-strain conditions.

No differences between grasses or seasons were found with respect to the proportions of vascular tissue (Table 5.7). The average of 20.7% for the four hays agrees with that reported by Akin (1986) for tropical grasses.

The proportion of mesophyll was affected by a grass x season interaction (P=.0019; Table 5.7). In June, Pensacola had higher (P=.0006) proportions of mesophyll than did Mott, but there were no differences between grasses in September. Mesophyll cells were less tightly arranged and more air spaces were present in Mott leaves compared to Pensacola, where some of the more external layers of parenchyma tissue had lignified cell walls (Figure 5.2).

Akin (1986, 1989) and Wilson et al. (1989a) have demonstrated that mesophyll and phloem are easily digested by rumen microorganisms due to their low lignin concentration, and that their proportions in the anatomical structure of blades is a good indication of how much of the

plant can be digested qickly during fermentation in the rumen of animals. When leaf cross sections were incubated in vitro for 24 h in rumen fluid:artificial saliva, most or all of the mesophyll tissue was digested in both grasses and disappeared from the microscopical area (Figure 5.3). Epidermal cell contents were well digested in both grasses. While about 50% of the epidermal cell wall disappeared by digestion in Mott, in the case of Pensacola most of the cell wall remained intact. Sclerenchyma fibers were not digested at all and in the case of Pensacola the girder structure was prevalent and maintained the integrity of the cross sectional area.

When quantities of epidermis, sclerenchyma and vascular tissues were expressed as proportions of the total residual tissue after digestion, residues of Pensacola were higher (P=.0001) in sclerenchyma and lower (P=.0001) in vascular tissue than were those of Mott (Table 5.8). There were differences in the proportion of epidermis between grasses only in June.

In Chapter IV, sheep fed Mott had higher frequency of chewing during eating and higher intake rate than did those fed Pensacola. It was suggested, according to Ulyatt et al. (1986), that such differences could be related to chemical or physical characteristics which made it more difficult to form a bolus before swallowing when Pensacola was fed. Chemical differences (Table 4.3) did not seem to be large enough to explain the observed differences between grasses. Anatomical differences observed in this experiment (girder structure and large proportions of sclerenchyma fibers) may be more involved in determining differences in mastication behavior during eating.

(A)

(B)

Figure 5.3. Micrographs (300x) of cross-sectional area of (A) Pensacola and (B) Mott leaf blades after 24 h of in vitro digestion with rumen fluid - artificial saliva mixture.

Table 5.8. Least squares means for the proportion (%) of epidermis, sclerenchyma and vascular tissues in the 24-hour in vitro digestion residue of Pensacola and Mott leaf blades harvested in June and September

Item	June		September			P-values[a]		
	Pens.	Mott	Pens.	Mott	SEM[b]	Grass (G)	Season (S)	G*S
Epidermis	55.4	42.7	46.0	44.8	2.86	.0237	.2140	.0582
		(.0025)[c]		(.7792)				
Sclerenchyma	11.3	3.9	14.3	4.2	1.17	.0001	.1701	.2738
Vasc. bundle	33.2	53.4	39.7	51.0	2.74	.0001	.4422	.1219

[a] Probability level for main effects and interaction.
[b] Standard error of means.
[c] Probability level for differences between grasses within season.

On the other hand, different patterns of digestion, due to differences in tissue accessibility to microorganisms, may have produced changes in anatomical structure that resulted in digested residues having different physical characteristics. Larger proportions and more widely distributed sclerenchyma fibers in Pensacola residues may have influenced mastication behavior during rumination, requiring larger numbers of jaw movements per bolus, and more ruminating time per kg of OM and NDF intake, as was observed in Chapter IV.

Relationships Between Intake, Digestibility and MRT

Intake of DM, OM and NDF, expressed either as total daily intake (g/d) or on a BW basis (g/kg BW), were not correlated with digestibility (Table 5.9). As would be expected relationships were improved when digestible DM or OM intake were related to DM or OM digestibility (Table 5.10). Strongly positive relationships between total DM or OM intake and digestibility have been reported (Blaxter et al., 1961; Campling et al., 1962; Minson, 1971; Van Soest, 1982). Results of this experiment contrast with those reports. Tropical grasses, like those used in this experiment, tend to have more variable patterns of response ranging from low to no relationship between intake and digestibility (Moore and Mott, 1973).

Relationships between MRT and intake existed only for small rumen digesta particles (Table 5.11). Mean retention time of rumen small particles correlated either with total or with digestible DM, OM or NDF intake; however, the correlations were higher with total nutrient intake. No relationship was detected between digestibility of DM or OM and any of the MRT values. The presence of negative relationships

Table 5.9. Correlations between voluntary intake and digestibility of dry matter (DM), organic matter (OM) and ash-free neutral-detergent fiber (NDF)

Intake	Digestibility		
	DM n=24	OM n=24	NDF n=24
g/d			
Dry matter	.31[a] .1347[b]	.16 .4401	.26 .2140
Organic matter	.21 .3318	.07 .7573	.16 .4466
Ash-free neutral-detergent fiber	.05 .8110	-.09 .6777	.01 .9767
g/kg BW			
Dry matter	.32 .1291	.18 .4111	.25 .2328
Organic matter	.20 .3608	.06 .7614	.14 .5201
Ash-free neutral-detergent fiber	.02 .9241	-.10 .6203	-.04 .8690

[a] Correlation coefficient (r).
[b] Probability level for r.

Table 5.10. Correlations between digestible fraction intake and
digestibility of dry matter (DM), organic matter (OM) and
ash-free neutral-detergent fiber (NDF)

	Digestibility (%)		
Intake	DM n=24	OM n=24	NDF n=24
g/d			
Digestible dry matter	.54[a] .0064[b]	.40 .0529	.48 .0161
Digestible organic matter	.45 .0284	.32 .1242	.41 .0454
g/kg BW			
Digestible dry matter	.57 .0038	.43 .0349	.50 .0134
Digestible organic matter	.46 .0235	.35 .0971	.41 .0457

[a] Correlation coefficient (r).
[b] Probability level for r.

Table 5.11. Correlations between digestibility or intake and mean
retention times of rumen small particles, entire hay and
liquid phase

	Mean retention time		
Item	Small n=24	Entire n=21	Liquid n=24
Digestibility (%) of:			
Dry matter	.01[a] .9741[b]	-.01 .9617	.15 .4883
Organic matter	.16 .4584	.04 .8677	.15 .4773
Intake (g/d) of:			
Dry matter	-.56 .0040	-.15 .5230	-.25 .2371
Organic matter	-.57 .0036	-.12 .5947	-.27 .1995
Ash-free neutral- detergent fiber	-.56 .0048	-.07 .7615	-.26 .2176
Intake (g/kg BW) of:			
Dry matter	-.55 .0052	-.08 .7449	-.27 .1965
Organic matter	-.54 .0059	-.03 .8810	-.30 .1616
Ash-free neutral- detergent fiber	-.52 .0095	.04 .8792	-.28 .1819
Digestible dry matter	-.49 .0159	-.08 .7327	-.20 .3566
Digestible organic matter	-.48 .0182	-.03 .8954	-.24 .2562
Digestible ash-free neutral-detergent fiber	-.46 .0250	.01 .9563	-.24 .2491

[a] Correlation coefficient (r). [b] Probability level for r.

between rumen small particles MRT and intake gives support to the suggestion that rather than the rate of particle size reduction, the critical step controlling intake is the passage of small particles (Ulyatt et al., 1986).

Relationships between total hay MRT and intake have been reported (Balch, 1950; Campling and Balch, 1961; Van Soest, 1982; Fisher et al., 1987). A more recent report (Cherney, 1989) indicates that the relationship between intake and MRT depended upon length and morphology of marked particles and, also, on the level of intake. The fact that no relationship existed between intake and entire hay MRT in this experiment may be explained, as referred to before, by the difficulties associated with the use of the Cr-mordanting technique for tracing the flow of large particles through the gastro-intestinal tract of ruminants.

From the results of this study it can be concluded that superior forage quality of Mott over Pensacola is due to higher OM digestibility and intake that resulted in higher digestible OM intake levels. It is suggested that the decline in grazing animal performance on Pensacola during late summer may be more closely associated with large reductions in intake rather than with changes in digestibility. Rumen small particles tended to be retained longer in the gastro-intestinal tract of animals fed Pensacola than of those fed Mott. Across grasses small-particle MRT was negatively correlated with voluntary intake. Longer MRT of small rumen digesta particles observed in animals fed Pensacola can explain the greater small-particle pool in the pre-feeding rumen digesta (Chapter IV) compared to animals fed Mott. The data support the

hypothesis that the size and dynamics of the small-particle pool pre-
feeding may be the main constraint for the achievement of higher levels
of intake in other tropical grasses.

Finally, Pensacola had a tighter arrangement of epidermal and
sclerenchyma tissues than did Mott, and in Pensacola sclerenchyma fiber
girder structures were present between the epidermis and vascular
bundles. These physical characteristics of the plant material may have
limited the rate of intake and frequency of chewing during eating and
increased energy expenditure by mastication during rumination.

Summary

Hays of 'Mott' dwarf elephantgrass (*Pennisetum purpureum* Schum.)
and 'Pensacola' bahiagrass (*Paspalum notatum* Flugge) harvested in June
(J) and September (S) were used in a 2x2 factorial arrangement in a
completely randomized design to determine the effect of grass species
and season of harvest on intake, digestibility, passage kinetics and
anatomical structure. Hays were offered ad libitum to 24 sheep for 14-d
adaptation and two collection periods (C-1= 7 d and C-2= 6 d). Small
particles (SP, <1.18 mm) collected from rumen digesta after a 20-h
fasting period, were mordanted with Cr (Cr-SP) and pulse dosed at the
beginning of C-1. Chromium-mordanted entire hay (Cr-H) and Co-EDTA were
dosed at the beginning of C-2. The proportion of different tissues was
digitized in cross sections of leaf blades before and after a 24-h in
vitro digestion with rumen liquor:artificial saliva. Intake and
digestibility of organic matter (OM) and ash-free neutral-detergent

fiber (NDF) were higher in Mott resulting in higher digestible OM intake levels compared to Pensacola (12.8 vs. 11.0 g/kg BW). Digestible OM intake was lower in September for both grasses but the seasonal effect was greater in Pensacola where digestible OM intake was reduced below maintenance. Pensacola Cr-SP tended (P=.124) to have larger mean retention time (MRT) than that of Mott (44.7 vs. 40.8 h), and across hays SP MRT was negatively related to OM intake (-.57, P=.004, n=24). No differences in Cr-H and Co-EDTA MRT were detected among treatments; however, MRT of Cr-H for Mott tended to be lower than that for Pensacola. Mott had more epidermis, less sclerenchyma and similar vascular tissue proportions compared to Pensacola, but after 24 h of in vitro digestion Pensacola had larger proportions of epidermis and sclerenchyma than did Mott. The results of this study indicate that superiority of Mott in forage quality is related to higher OM digestibilty and intake. Mean retention time of rumen SP may be one limiting factor controlling intake. Differences in anatomical structure not only affect digestibility but may also influence intake.

CHAPTER VI
GENERAL DISCUSSION AND CONCLUSIONS

This study suggests that the superiority of Mott over Pensacola in terms of animal performance may be a consequence of higher digestibility and voluntary intake. Further, the differences in quality may be explained by differences in anatomical structure of the grasses.

In vivo organic matter (OM) digestibility of Mott was higher than that of Pensacola, in spite of small differences in chemical composition between grasses. Differences in digestibility between forages of similar chemical composition indicate higher accessibility of ruminal microorganisms to potentially fermentable OM in plant material. Higher accessibility was supported by the greater proportion of potentially digestible ash-free neutral-detergent fiber (NDF) that was digested after 24 h in vitro, in the case of Mott compared to Pensacola. Lignin has classically been recognized as the major factor limiting cell-wall digestibility, but differences in its chemical composition, spatial distribution and partial digestion by anaerobic fungi in the rumen require a more detailed study of its role for each circumstance. Mott and Pensacola had similar total lignin concentration in the OM; furthermore, lignin represented the same proportion of acid-detergent fiber in both grasses. Consequently, lignin concentration could not be used to predict digestibility across species in this study.

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Voluntary intake is controlled mainly by the distention or physical control mechanism when animals are fed diets based on forages. Thus, animals will consume different diets up to a common point of rumen fill which is considered constant and determined by the physical capacity of the animal. The level of forage intake will then be determined by the rate at which rumen fill is released. Rumen fill can be released by two mechanisms, digestion which transforms OM into gas and absorbable acids, and passage out of the rumen of undigested material. It would be expected that the higher the fermentability of the forage the higher its level of intake, but this is not always the case.

No differences between grasses were observed in the disappearance of nutrients from rumen digesta during eating, but after feeding more OM and NDF disappeared from the rumen digesta of animals fed Mott than from those fed Pensacola. The differences in OM and NDF disappearance were not accompanied by differences in the disappearance of indigestible NDF among hays, suggesting that more fill could be released by digestion in the case of Mott than in the case of Pensacola. These observations support the in vitro tests.

Undigested forage residue present in the rumen must be reduced in particle size to about 1.18 mm in order to increase the probability of their escaping from the rumen through the reticulo-omasal orifice and contributing to the release of fill. Comminution of particles occurs mainly by mastication during eating and rumination. All particles of less than 1.18 mm do not necessarily escape. Most of the time more than 50% of the particulate phase in the rumen consists of particles smaller

than 1.18 mm. Retention of small particles may be due to entrapment in the large particle mat or because small particles do not have a specific gravity heavy enough to be close to the reticulo-omasal orifice in order to be propelled out of the rumen.

Efficiency of particle size reduction was the same for both grasses during eating and rumination, but animals receiving Mott spent less time ruminating and had a smaller number of ruminating jaw movements per kg of OM or NDF consumed. Furthermore, the pre-feeding large-particle pool in animals receiving Pensacola was larger than that of those receiving Mott, indicating that the final efficiency was lower in the case of Pensacola. These observations were confirmed by the estimation of different indexes like NDF turnover, rumination index and specific fragility.

Greater pre-feeding small-particle pools found in animals receiving Pensacola hays indicated either entrapment of small particles or failure of digestion to give small particles the specific gravity required to reach the point of escape. Greater large-particle pools in Pensacola-fed animals as well as lower digestibility may have acted together in retaining larger quantities of small particles compared to those receiving Mott.

Under restricted feeding, the weight of pre-feeding small-particle pools in the rumen of animals fed Pensacola were equivalent to almost 65% of the daily NDF allowance, compared to 45% for those fed Mott. Mean retention time of the small particles collected from the rumen digesta pre-feeding, and fed to animals fed ad libitum, tended to be

larger in animals consuming Pensacola, and was negatively related to intake.

Analysis of the anatomical characteristics of these two grasses indicated the presence of "girder structures" in leaves of Pensacola but not in those of Mott. Girder structures are formed by sclerenchyma fibers connecting epidermis and vascular bundles, and the girder remained intact after 24 h of in vitro digestion with rumen microorganisms. The presence of a girder structure indicates strong resistance not only to digestion but also to particle size reduction during rumination, because it has been found that epidermis and sclerenchyma are the tissues most responsible for the stiffness and load-bearing characteristics of grass leaves.

In light of the results of this work it is concluded that differences in forage quality between grasses can be explained at the anatomical level by understanding the dynamic and mechanical interactions between microscopic structures and biological processes. Basic differences in anatomical characteristics and spatial distribution of fibrous materials in forage plants can contribute substantially to differences in access of rumen microorganisms to fermentable material. Lower accessibility during fermentation is translated into low in vitro and in vivo digestibility. In addition ruminal retention of less digestible material having the hardest anatomical structures will affect mastication patterns in that more chewing effort will be required per unit of feed per day. Increased chewing effort may result in larger energetic losses and reduced efficiency of nutrient utilization. Also, if particle size reduction is less effective, the residual pre-feeding

rumen pool will increase retention time of those particles that have the size required for escaping the rumen creating physical limits to larger levels of intake.

General implications for research

The presence of grass x age interactions in the plot experiment with respect to IVOMD and N indicated differences in the process of maturation between these two grasses which need to be better understood. Suggested agronomic research may include studies of growth and tillering as well as more detailed work on changes in the chemical composition of cell walls during regrowth.

The area of plant anatomy and its relation to changes in forage quality should be explored more. Using Mott as a prototype high quality species may allow more specific definition of plant characteristics which affect quality, particularly of tropical grasses. Generated information in the future could eventually be used in the rapid prediction of forage quality of different plant materials.

The importance of mastication is evident in the process of particle comminution and control of voluntary intake. It is recommended to include in future similar experiments, levels of ad libitum intake in order to gain information more closely related to normal situations.

Evaluation of Mott and other tropical grasses should consider the study of differences in the efficiency of utilization of absorbed nutrients, particularly when hays are offered to growing animals. Finally, it would be interesting to continue studying ruminal small particles as a determinant of passage and intake. Results of this work indicate that the magnitude of the residual pool in the rumen prior to

the next meal is determined by the type of forage and, also, that MRT is associated with intake. More information needs to be generated on this point using different grasses.

APPENDICES

Table A3.1. Mean squares for dry matter yield, proportion of leaf blade, nitrogen (N) concentration and in vitro organic matter digestibility (IVOMD) in stem and total canopy of Pensacola and Mott grasses harvested at three ages in June and September

				Stem		Canopy	
Source	df	DM yield	leaf blade%	N	IVOMD	N	IVOMD
Grass,G	1	1.5332 (.0110)[a]	2447.8860 (.0009)	2.4806 (.0006)	2240.4444 (.0001)	3.3737 (.0002)	2168.4058 (.0001)
B(G)[b]	4	0.0765 (.1691)	32.0344 (.1295)	0.0248 (.2585)	1.7003 (.5564)	0.0191 (.6054)	2.1466 (.0473)
Age,A	2	9.8447 (.0001)	18.4039 (.0219)	0.7902 (.0001)	55.3169 (.0088)	2.9887 (.0001)	276.9809 (.0001)
A*G	2	0.2147 (.3465)	7.8626 (.1245)	0.2669 (.0051)	4.4619 (.5109)	0.3982 (.0031)	12.9974 (.0316)
A*B(G)[c]	8	0.1769 (.0185)	2.8764 (.9764)	0.0243 (.2628)	6.1009 (.0779)	0.0309 (.4221)	2.3682 (.0267)
Season,S	1	11.1965 (.0001)	2648.0488 (.0001)	0.0017 (.7185)	15.6025 (.2466)	0.5391 (.0066)	25.6406 (.0025)
S*G	1	1.1388 (.0011)	1574.2513 (.0002)	0.0006 (.8278)	16.0000 (.2417)	0.0155 (.4294)	7.3352 (.0227)
S*B(G)[d]	4	0.0159 (.7749)	8.5162 (.6401)	0.0116 (.5790)	8.4867 (.0451)	0.0202 (.5830)	0.5650 (.4462)
S*A	2	1.3426 (.0001)	21.2440 (.2543)	0.0096 (.5555)	6.6908 (.0975)	0.0832 (.1001)	9.3628 (.0003)
S*A*G	2	0.2340 (.0210)	4.1852 (.7339)	0.0119 (.4908)	1.0808 (.6186)	0.0931 (.0818)	18.6635 (.0001)
Residual	8	0.0360	13.0128	0.0152	2.1181	0.0267	0.5464
C.V.		8.6	4.4	9.5	2.7	8.4	1.3
R^2		0.99	0.98	0.98	0.99	0.98	0.99

[a] Probability level.
[b] B(G) = Block(Grass); error term for G.
[c] Error term for A and A*G.
[d] Error term for S and S*G.

Table A3.2. Mean squares for laboratory characteristics of leaf blades
of Pensacola and Mott grasses harvested at three ages in
June and September

Source	df	N[a]	IVOMD[b]	NDF[c]	Lignin	Cellulose
Grass,G	1	1.9834 (.0005)[d]	2115.2334 (.0001)	601.4756 (.0001)	2.8617 (.0119)	30.1584 (.0026)
B(G)[e]	4	0.0180 (.6675)	2.5442 (.0824)	0.4939 (.9327)	0.1490 (.2314)	0.6703 (.1891)
Age,A	2	3.3263 (.0001)	336.1896 (.0001)	42.7272 (.0001)	0.8176 (.0034)	11.6942 (.0001)
A*G	2	0.3780 (.0047)	10.0426 (.0552)	52.0190 (.0001)	0.3367 (.0363)	10.8384 (.0001)
A*B(G)[f]	8	0.0336 (.4293)	2.3618 (.0794)	0.7201 (.9511)	0.0652 (.6421)	0.0962 (.9523)
Season,S	1	0.1284 (.0768)	22.4834 (.0083)	0.0156 (.9126)	4.9506 (.0001)	10.5084 (.0152)
S*G	1	0.0506 (.2108)	9.4556 (.0344)	7.6084 (.0615)	0.1667 (.0465)	0.0667 (.7617)
S*B(G)[g]	4	0.0228 (.5717)	0.9512 (.3996)	1.1451 (.7647)	0.0206 (.9068)	0.6332 (.2075)
S*A	2	0.0805 (.1250)	6.1651 (.0149)	1.5464 (.5624)	0.0890 (.3948)	2.2459 (.0198)
S*A*G	2	0.0869 (.1101)	21.0994 (.0003)	3.8146 (.2743)	0.1842 (.1770)	0.7909 (.1576)
Residual	8	0.0295	0.8267	2.4980	0.0850	0.3368
C.V.		8.2	1.6	2.1	6.9	1.7
R[2]		0.98	0.99	0.98	0.95	0.97

[a] Nitrogen; [b] In vitro organic matter digestibility.
[c] Ash-free neutral-detergent fiber.
[d] Probability level.
[e] B(G) = Block(Grass); error term for G.
[f] Error term for A and A*G.
[g] Error term for S and S*G.

Table A3.3.   Mean squares for DM yield, total canopy (TIVOMD) and leaf
blade (LIVOMD) in vitro OM disappearance in Pensacola and
Mott grasses harvested in June and September

Source	df	Pensacola			Mott		
		DM yield	TIVOMD	LIVOMD	DM yield	TIVOMD	LIVOMD
Block,B	2	0.0483	2.0760	2.7679	0.1046	2.2171	2.3206
		(.4065)[a]	(.1759)	(.2264)	(.1297)	(.0558)	(.0650)
Season,S	1	9.7385	30.2021	30.5501	2.5968	2.7737	1.3889
		(.0007)	(.0221)	(.0526)	(.0096)	(.1286)	(.0988)
S*B[b]	2	0.0065	0.6907	1.7418	0.0254	0.4394	0.1606
		(.8628)	(.4688)	(.3488)	(.4883)	(.3716)	(.6919)
Age,A	2	6.2746	92.2642	127.6554	3.7849	197.7140	218.5768
		(.0002)	(.0003)	(.0004)	(.0002)	(.0001)	(.0001)
A*B	4	0.0334	3.8423	3.7696	0.3204	0.8940	0.9541
		(.5896)	(.0713)	(.1562)	(.0200)	(.1880)	(.2083)
A*S	2	1.2207	21.6541	20.3010	0.3559	6.3722	6.9635
		(.0042)	(.0042)	(.0121)	(.0201)	(.0094)	(.0105)
Residual	4	0.0425	0.7499	1.2564	0.0294	0.3430	0.3970
C.V.		8.6	1.8	2.3	8.6	0.9	1.0
R^2		0.99	0.99	0.98	0.99	0.99	0.99

[a] Probability level.
[b] Error term for S.

Table A4.1. Mean squares for ash-free neutral-detergent fiber (NDFI) and organic matter (OMI) intake, and total time spent eating by sheep fed Pensacola and Mott hays harvested in June and September

Source	df	NDFI	OMI	Time Eating
Period	3	2.3694 (.1215)[a]	4.4304 (.0817)	584.5578 (.2550)
Animal	3	0.5035 (.6256)	0.9539 (.5407)	33.8307 (.0091)
Grass,G	1	0.3579 (.5305)	8.3320 (.0390)	288.1821 (.3880)
Season,S	1	0.9814 (.3127)	0.5808 (.5131)	287.2021 (.3887)
S*G	1	1.0594 (.2959)	2.8074 (.1774)	114.1326 (.5795)
Residual	6	0.8082	1.2027	332.7941
C.V.		7.4	6.8	11.3
R^2		0.69	0.79	0.86

[a] Mean square (Probability level).

Table A4.2. Mean squares for intake rate, and number of jaw movements
per kilogram of organic matter (OMI) or ash-free neutral-
detergent fiber (NDFI) intakes during eating by sheep fed
Pensacola and Mott hays harvested in June and September

		Intake	Jaw movements		
Source	df	Rate	/min	/OMI	/NDFI
Period	3	0.1795[a] (.8974)	78.3954 (.0809)	1.0919 (.9399)	0.8531 (.9811)
Animal	3	4.4505 (.0493)	52.9462 (.1564)	137.5754 (.0028)	245.9239 (.0029)
Grass,G	1	4.3058 (.0749)	548.7306 (.0022)	19.4193 (.1817)	3.0187 (.6727)
Season,S	1	0.3715 (.5506)	96.5306 (.0766)	17.2564 (.2044)	22.8693 (.2677)
S*G	1	1.9850 (.1942)	18.0625 (.3913)	17.9957 (.1962)	27.8632 (.2262)
Residual	6	0.9295	21.1706	8.5143	15.3268
C.V.		20.7	4.5	12.3	12.5
R^2		0.79	0.89	0.90	0.90

[a] Mean square (Probability level).

Table A4.3. Mean squares for total rumination time per day (TRUMEAN)
           and rumination time spent per kg of organic matter (TRUOM)
           or ash-free neutral-detergent fiber (TRUNDF) intake, during
           rumination, and rumination index by sheep fed Pensacola and
           Mott hays harvested in June and September

Source	df	TRUMEAN	TRUOM	TRUNDF	Rum. Index
Period	3	3207.6205[a]	0.0218	0.0336	528.6703
		(.1959)	(.0441)	(.0461)	(.0148)
Animal	3	20150.3671	0.0386	0.0651	1217.2253
		(.0045)	(.0124)	(.0105)	(.0023)
Grass,G	1	383.6700	0.0360	0.0304	2023.9149
		(.6306)	(.0277)	(.0785)	(.0017)
Season,S	1	9.6758	0.00002	0.0001	14.6474
		(.9385)	(.9539)	(.9063)	(.6637)
S*G	1	964.7903	0.0107	0.0161	783.6008
		(.4525)	(.1656)	(.1740)	(.0156)
Residual	6	1495.8378	0.0043	0.0068	70.1137
C.V.		12.0	14.5	13.8	10.8
R^2		0.89	0.90	0.89	0.95

[a] Mean square (Probability level).

Table A4.4. Mean squares for rumination constants per bolus in sheep
            fed Pensacola and Mott hays harvested in June and September

Source	df	Jaw movements /bolus	Time(sec) /bolus	Rate[a]
Period	3	53.0625[b] (.4349)	9.4683 (.6366)	0.0135 (.2494)
Animal	3	70.5075 (.3309)	65.3950 (.0649)	0.0089 (.3957)
Grass,G	1	183.6025 (.1047)	74.8225 (.0718)	0.0033 (.5333)
Season,S	1	40.3225 (.4052)	11.2225 (.4303)	0.0018 (.6426)
S*G	1	122.1025 (.1703)	28.0900 (.2295)	0.0126 (.2436)
Residual	6	50.3233	15.7008	0.0076
C.V.		13.5	9.4	7.0
R^2		0.70	0.78	0.65

[a] Rate = Number of jaw movements/Time.
[b] Mean square (Probability level).

Table A4.5. Mean squares for proportion of large particles in rumen digesta and total large- and small-particles pools before and after 4-hour feeding period in sheep fed Pensacola and Mott hays harvested in June and September

				Particle pools (g/kg BW)			
		Large %		Large		Small	
Source	df	Pre	Post	Post	Pre	Post	Pre
Period	3	36.0286[a] (.5062)	15.1808 (.3311)	0.5001 (.8490)	0.3700 (.6022)	1.3193 (.4230)	0.3780 (.9338)
Animal	3	3.3436 (.9731)	86.4108 (.0019)	6.1998 (.1007)	1.5646 (.1293)	5.5585 (.0538)	7.0766 (.1490)
Grass,G	1	9.7903 (.6453)	132.8450 (.0036)	2.0473 (.3384)	3.2481 (.0518)	10.9893 (.0237)	25.6650 (.0222)
Season,S	1	27.1953 (.4449)	3.3800 (.6084)	5.1873 (.1489)	1.1342 (.2025)	1.3227 (.3364)	.5724 (.6638)
S*G	1	64.6953 (.2430)	6.4800 (.4793)	4.3425 (.1806)	3.0563 (.0572)	3.7302 (.1299)	1.9334 (.4332)
Residual	6	44.9393	12.5109	1.8925	0.5544	1.2119	2.7416
C.V.		23.5	5.6	12.1	28.3	16.2	25.1
R^2		0.18	0.62	0.74	0.80	0.83	0.75

[a] Mean square (Probability level).

Table A4.6. Mean squares for the efficiency of mastication, ash-free
neutral-detergent fiber dynamics in the rumen, and specific
fragility for Pensacola and Mott hays harvested in June and
September

Source	df	Effic. eating	# bolus /day	NDF retained	NDF turnover	Effic. rumint.	Specific fragility
Period	3	122.6057[a]	3615.4897	14.9061	0.3014	13.0036	0.0318
		(.4471)	(.6355)	(.5282)	(.1409)	(.9152)	(.4349)
Animal	3	82.8250	18877.6725	52.7708	0.4766	602.0030	0.0423
		(.5909)	(.1072)	(.1234)	(.0630)	(.0176)	(.3309)
Season,S	1	20.6971	881.5231	6.2894	0.0095	1.0583	0.0242
		(.6925)	(.7142)	(.5777)	(.7811)	(.9111)	(.4052)
Grass,G	1	0.1247	3000.2643	38.1194	0.4201	231.4246	0.1102
		(.9753)	(.5052)	(.1976)	(.1017)	(.1360)	(.1047)
S*G	1	3.8357	30.4534	0.4614	0.0143	1.5720	0.0733
		(.8641)	(.9454)	(.8786)	(.7339)	(.8918)	(.1703)
Residual	6	120.1456	5975.5856	18.1648	0.1127	78.1322	0.0302
C.V.		39.4	16.8	19.4	18.4	21.1	12.4
R^2		0.47	0.66	0.70	0.80	0.82	0.70

[a] Mean square (Probability level).

Table A4.7. Mean squares for different chemical components of rumen
digesta expressed per unit of body weight (g/kg BW), before
a 4-hour feeding period in sheep fed Pensacola and Mott hays
harvested in June and September

Source	df	DM[a]	OM[b]	NDF[c]	INDF[d]
Period	3	2.2653[e] (.6779)	2.3630 (.6430)	0.9951 (.7835)	0.2356 (.9089)
Animal	3	35.9023 (.0144)	28.6735 (.0207)	15.2484 (.0365)	11.7909 (.0129)
Grass,G	1	35.9366 (.0273)	43.7301 (.0162)	47.1736 (.0061)	24.0438 (.0055)
Season,S	1	3.8413 (.3796)	4.1729 (.3463)	3.3181 (.3144)	1.5198 (.3278)
S*G	1	14.1042 (.1191)	14.7220 (.1034)	9.8515 (.1074)	4.2452 (.1253)
Residual	6	4.2716	3.9962	2.7529	1.3394
C.V.		13.9	15.7	18.0	15.3
R^2		0.87	0.87	0.87	0.89

[a] DM = dry matter.
[b] OM = organic matter.
[c] NDF = ash-free neutral-detergent fiber.
[d] INDF = Indigestible NDF (144 h in vitro digestion residue).
[e] Mean square (Probability level).

Table A4.8. Mean squares for different chemical components of rumen digesta expressed per unit of body weight (g/kg BW), after a 4-hour feeding period in sheep fed Pensacola and Mott hays harvested in June and September

Source	df	DM[a]	OM[b]	NDF[c]	INDF[d]
Period	3	4.4515[e] (.6203)	4.0674 (.6026)	2.8505 (.5338)	0.91047 (.7069)
Animal	3	41.9137 (.0312)	33.5999 (.0370)	17.6528 (.0451)	11.9380 (.0278)
Grass,G	1	2.9756 (.5395)	12.2004 (.2071)	22.5232 (.0449)	28.2948 (.0084)
Season,S	1	16.5801 (.1756)	16.2876 (.1534)	11.7488 (.1178)	3.2923 (.2359)
S*G	1	22.7256 (.1224)	21.2234 (.1115)	16.1221 (.0764)	7.5067 (.0939)
Residual	6	7.0330	6.1020	3.5272	1.8984
C.V.		9.8	10.4	10.3	14.0
R^2		0.81	0.82	0.84	0.87

[a] DM = dry matter.
[b] OM = organic matter.
[c] NDF = ash-free neutral-detergent fiber.
[d] INDF = Indigestible NDF (144 h in vitro digestion residue).
[e] Mean square (Probability level).

Table A4.9. Chemical composition of rumen digesta before and after 4-hour feeding period in sheep fed Pensacola and Mott hays harvested in June and September

	Pensacola		Mott			P-values[a]		
						Grass	Season	
Time	June	Sept	June	Sept	SEM[b]	(G)	(S)	G*S

——— Dry matter (%) ———								
Pre-feeding	10.4	8.4	7.3	7.6	0.48	.0062	.1155	.0526
		(.0239)[c]		(.2861)				
Post-feeding	11.2	10.0	10.2	9.6	0.35	.0819	.0411	.3855
—— Organic matter (% dry matter) ——								
Pre-feeding	89.2	86.5	82.4	83.4	0.80	.0009	.3245	.0650
		(.0568)		(.4354)				
Post-feeding	89.6	88.3	85.3	85.4	0.52	.0004	.2775	.2296
Ash-free ——Neutral-detergent fiber (% OM)——								
Pre-feeding	76.8	74.6	67.4	67.8	0.62	.0001	.2104	.0812
		(.0483)		(.6425)				
Post-feeding	79.6	78.4	74.5	74.8	0.22	.0001	.1157	.0145
		(.0101)		(.3124)				
Indigestible neutral-detergent fiber[d] (% organic matter)								
Pre-feeding	61.4	61.1	57.4	56.8	1.85	.0681	.8311	.9432
Post-feeding	45.8	44.5	36.5	38.0	0.82	.0001	.9300	.1381

[a] Probability levels for main effects and interaction.
[b] Standard error of means.
[c] Probability level for differences between seasons within grass.
[d] Indigestible NDF = Residue after 144 h of in vitro digestion.

Table A4.10. Mean squares for different chemical components of rumen
digesta before a 4-hour feeding period in sheep fed
Pensacola and Mott hays harvested in June and September

Source	df	DM[a]	OM[b]	NDF[c]	INDF[d]
Period	3	1.0156[e]	6.0406	1.9190	11.2373
		(.4224)	(.1731)	(.3667)	(.5288)
Animal	3	6.1406	25.5373	6.2873	25.6973
		(.0251)	(.0098)	(.0652)	(.2349)
Grass,G	1	15.8006	97.5156	263.2506	67.6506
		(.0062)	(.0009)	(.0001)	(.0681)
Season,S	1	3.1506	2.9756	2.9756	0.6806
		(.1155)	(.3245)	(.2104)	(.8311)
S*G	1	5.4056	13.1406	6.6306	0.0756
		(.0526)	(.0650)	(.0812)	(.9432)
Residual	6	0.9315	2.5848	1.5131	13.7148
C.V.		11.4	1.9	1.7	6.3
R^2		0.89	0.93	0.97	0.68

[a] DM = Dry matter.
[b] OM = Organic matter.
[c] NDF = Ash-free neutral-detergent fiber.
[d] INDF = Indigestible NDF (144 h in vitro digestion residue).
[e] Mean square (Probability level).

Table A4.11. Mean squares for different chemical components of rumen
digesta after a 4-hour feeding period in sheep fed
Pensacola and Mott hays harvested in June and September

Source	df	DM^a	OM^b	NDF^c	$INDF^d$
Period	3	0.1517^e (.8150)	4.0317 (.0819)	0.1790 (.4989)	1.4500 (.6718)
Animal	3	1.4517 (.1164)	6.1650 (.0354)	2.4123 (.0061)	22.9617 (.0138)
Grass,G	1	2.1025 (.0819)	52.5625 (.0004)	76.1256 (.0001)	251.2225 (.0001)
Season,S	1	3.2400 (.0411)	1.5625 (.2775)	0.6806 (.1157)	0.0225 (.9300)
S*G	1	0.4225 (.3855)	1.9600 (.2296)	2.3256 (.0145)	7.8400 (.1381)
Residual	6	0.4825	1.0958	0.2015	2.6817
C.V.		6.8	1.2	0.6	4.0
R^2		0.78	0.93	0.99	0.95

[a] DM = Dry matter.
[b] OM = Organic matter.
[c] NDF = Ash-free neutral-detergent fiber.
[d] INDF = Indigestible NDF (144 h in vitro digestion residue).
[e] Mean square (Probability level).

Table A4.12. Mean squares for nutrient disappearance from the rumen digesta, during eating and during rumination, in sheep fed Pensacola and Mott hays harvested in June and September

Source	df	During eating			During rumination		
		OM[a]	NDF[b]	INDF[c]	OM	NDF	INDF
Period	3	6.9672[d]	3.0958	0.1641	3.1626	1.8632	0.8121
		(.0939)	(.2173)	(.7307)	(.3180)	(.3013)	(.7253)
Animal	3	2.7721	1.5385	0.1546	2.5964	1.5551	0.2882
		(.3424)	(.4592)	(.7462)	(.3888)	(.3651)	(.9192)
Grass,G	1	0.0545	2.3232	0.1684	9.7342	4.5048	0.1729
		(.8756)	(.2677)	(.5338)	(.0788)	(.1023)	(.7669)
Season,S	1	1.5152	0.3787	1.5723	3.9721	2.5795	0.3383
		(.4223)	(.6394)	(.1063)	(.2253)	(.1963)	(.6795)
S*G	1	0.8201	0.0233	0.4735	0.5928	0.7683	0.4616
		(.5498)	(.9066)	(.3178)	(.6203)	(.4579)	(.6303)
Residual	6	2.0435	1.5572	0.3642	2.1753	1.2211	1.7964
C.V.		27.6	39.3	46.0	13.5	12.3	58.8
R^2		0.72	0.64	0.73	0.71	0.71	0.28

[a] OM = Organic matter.
[b] NDF = Ash-free neutral-detergent fiber.
[c] INDF = Indigestible NDF (144 h in vitro digestion residue).
[d] Mean square (Probability level).

Table A5.1. Statistics for the Cr excretion curve by sheep in pen 2 fed
Mott harvested in September (Figure 5.1)

Non-linear Least Square Summary Statistics

Source	df	Sum Squares	Mean Square
Regression	4	96179.1105	24044.7776
Residual	14	154.8034	11.0574
Uncorrected total	18	96333.9139	
(Corrected total)	17	50599.9452	

Parameter	Estimate	Asymptotic Standard Error	Asymptotic 95% Confidence interval Lower	Upper
K_1	.4083	.0277	.3488	.4678
K_2	.0420	.0016	.0385	.0455
Lag	7.9973	.1907	7.5883	8.4063

Season	Grass	Pen	Time	Observed	Adjusted	Residual
Sept.	Mott	2	2	3.05	0.00	3.05
			6	2.73	0.00	2.73
			10	40.36	40.82	-0.46
			14	133.90	132.86	1.05
			18	154.91	153.28	1.03
			22	134.46	141.83	-7.37
			27	121.56	118.4	3.16
			33	95.74	92.63	3.11
			39	77.08	72.06	5.02
			45	56.09	56.02	0.07
			54	34.42	38.39	-3.97
			66	19.62	23.19	-3.57
			78	12.00	14.01	-2.01
			90	8.11	8.46	-0.35
			102	5.74	5.11	0.63
			114	2.62	3.09	-0.47
			126	3.22	1.87	1.35
			138	2.29	1.29	1.00

Table A5.2. Mean squares for dry matter (DMD), organic matter (OMD) and
ash-free neutral-detergent fiber (NDFD) digestibilities of
Pensacola and Mott hays harvested in June and September

Source	df	DMD	OMD	NDFD
Grass,G	1	252.9915[a] (.0001)	157.1592 (.0001)	290.0581 (.0001)
Season,S	1	12.3227 (.0578)	16.9113 (.0317)	10.8237 (.1229)
G*S	1	11.9674 (.0612)	19.6092 (.0219)	62.9465 (.0009)
Error	20	3.0418	3.1718	4.1720
C.V.		2.8	2.8	2.9
R^2		0.82	0.75	0.81

[a] Mean square (Probability level).

Table A5.3. Mean squares for Quality index (QI) and total and digestible
organic matter and ash-free neutral-detergent fiber intake
of Pensacola and Mott hays harvested in June and September

Source	df	Q.I.	Organic matter		Neutral-detergent fiber	
			total	digestible	total	digestible
Grass,G	1	0.4582[a]	45.1349	46.5821	7.0811	19.9747
		(.0001)	(.0161)	(.0003)	(.2112)	(.0039)
Season,S	1	0.2136	63.0434	19.27028	34.4398	14.2797
		(.0042)	(.0056)	(.0112)	(.0076)	(.0121)
G*S	1	0.0015	5.0339	0.2136	3.3831	0.0069
		(.7872)	(.3904)	(.7718)	(.3826)	(.9523)
Error	20	0.0205	6.5302	2.4657	4.2448	1.8766
C.V.		12.0	13.3	12.7	14.0	13.4
R^2		0.62	0.46	0.57	0.36	0.48

[a] Mean square (Probability level).

Table A5.4. Mean squares for lag and mean retention time of rumen small particles, liquid phase, and entire hay of Pensacola and Mott hays harvested in June and September

Source	df	Lag		Mean retention time		
		Small	Liquids	Small	Liquids	Entire
Grass,G	1	5.1700 (.1613)	0.9205 (.3812)	92.6818 (.1245)	0.0933 (.8014)	66.6625 (.1203)
Season,S	1	1.0289[a] (.5238)	2.1283 (.1885)	120.2255 (.0824)	3.8035 (.1192)	0.0522 (.9714)
G*S	1	0.8063 (.5721)	0.9056 (.3850)	1.8266 (.8242)	0.0158 (.9175)	6.4446 (.6907)
Error	20[b]	2.4436	1.1480	36.0378	1.4354	39.3287
C.V.		18.6	12.5	14.0	6.6	11.0
R^2		0.13	0.15	0.23	0.12	0.10

[a] Mean square (Probability level).
[b] df = 17 for Mean retention time of entire hay.

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Table A5.5. Mean squares for proportions of epidermis (EPID),
sclerenchyma (SCL), vascular bundle (VB) and mesophyll
(MSPH) in leaf blades of 5-week Pensacola and Mott grasses
harvested in June and September

Source	df	EPID	SCL	VB	MSPH
Grass,G	1	358.2448 (.0001)[a]	113.7356 (.0001)	0.6934 (.7865)	53.0812 (.0604)
Season,S	1	3.4319 (.4317)	0.6348 (.4543)	13.7187 (.2339)	34.2472 (.1272)
S*G	1	44.4834 (.0077)	1.4924 (.2544)	23.3745 (.1235)	161.9495 (.0019)
Error	28	5.3913	1.1023	9.2683	13.8596
C.V.		8.1	27.1	14.9	7.9
R^2		0.73	0.79	0.13	0.38

[a] Mean square (Probability level).

Table A5.6. Mean squares for the proportion of epidermis (EPID),
sclerenchyma (SCL) and vascular bundle (VB) in the 24-hour
in vitro digestion residue of 5-week Pensacola and Mott
leaf blades collected in June and September

Source	df	EPID	SCL	VB
Grass,G	1	307.7205 (.0237)[a]	470.1218 (.0001)	1740.1859 (.0001)
Season,S	1	85.3584 (.2140)	17.5412 (.1701)	29.2155 (.4422)
S*G	1	208.1349 (.0582)	10.9862 (.2738)	123.4769 (.1219)
Error	22	52.1163	8.7193	47.6935
C.V.		15.2	35.2	15.6
R^2		0.37	0.73	0.64

[a] Mean square (Probability level for F-value).

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Jorge Antonio Flores Caceres was born on 2 November 1950, in Lima, Peru. He was raised in Lima until graduating from Colegio Guadalupe in 1966, and he received his B.S. degree in veterinary sciences from the University of San Marcos in 1973.
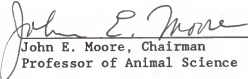
Upon graduation Jorge Antonio entered the Graduate School of University of San Carlos in Guatemala, where he worked under Drs. Ricardo Bressani and Marco T. Cabezas in the Center for Advanced Studies in Nutrition and Food Science (CESNA-INCAP), receiving his M.S. degree in Food Sciences and Animal Nutrition in 1978.

Jorge Antonio worked for INCAP as an associate researcher in the field of forages and ruminant nutrition with projects in Guatemala and El Salvador until 1980, when he moved to Honduras to work for the government in the area of research of agricultural by-products. In 1982 he was appointed as Associate Professor in the Animal Science Department of Panamerican School of Agriculture 'El Zamorano'.
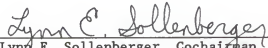
Jorge Antonio enrolled at the University of Florida in the fall of 1986 and has worked as a research assistant until 1990. He is currently a candidate for the Doctor of Philosophy degree and is member of Gamma Sigma Delta, the honor society of agriculture.

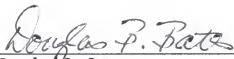Jorge Antonio is married to Gladys and they have two children, Fabricio and Valeria.
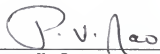
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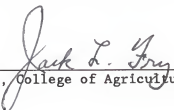
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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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